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On the Structure of the Mammal-Like Reptiles of the Sub-Order Gorgonopsia

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VIII. *On the Structure of the Mammal-like Reptiles of the Sub-order Gorgonopsia.*

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(PLATES 27–34.)

Over eighty years ago reptiles with a mammal-like dentition were first discovered in South Africa by ANDREW GEDDES BAIN, and specimens were sent to England in 1853. One of these, a fairly well preserved and nearly complete skull, was described by OWEN in 1860 under the name *Galesaurus planiceps*. In 1876 OWEN published a Catalogue of the South African Fossil Reptiles, and gave good figures of all the important remains of mammal-like reptiles that had been received by the British Museum up to that date. A considerable number of genera and species were described, and these were placed in three groups, the Mononarialia, the Binarialia, and the Tectinarialia, and the three groups were united into an order, the Theriodontia.

Although OWEN pointed out mammalian affinities in these Theriodonts it was only some years later that he definitely suggested that the mammals may have been descended from some one of the South African mammal-like reptiles. About the same time COPE, in America, was pointing out the mammalian affinities of the allied Pelycosaurs; and, although forty years ago the scientific world was rather inclined to follow the view of HUXLEY, that the mammalian ancestor was an Amphibian, the importance of the South African fossil reptiles was becoming more and more realised.

In 1888 SEELEY came out to South Africa, and under the guidance of Mr. T. BAIN made a tour through Cape Colony. Mr. BAIN, like his father, had for many years been interested in fossil reptiles and had sent numerous specimens to the British Museum. He had a first-hand knowledge of the principal hunting grounds, and knew of all the important collections that had been made by residents in the Colony. Through introductions to the great collectors Dr. KANNEMEYER of Burghersdorp and Mr. ALFRED BROWN of Aliwal North, SEELEY obtained good specimens of new types of carnivorous Theriodonts. These, together with specimens in the Albany Museum mostly collected by KANNEMEYER, and others collected in the Queenstown district, were well described and figured by SEELEY and resulted in a great addition to our knowledge of the Theriodonts.

Most of these specimens from the North-East of the Colony were from beds of much later date than those fossils which had been collected by Mr. A. G. BAIN and his son Mr. T. BAIN, and it was therefore not surprising that SEELEY discovered among them some strikingly new forms. He found some large carnivorous types with cusped

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molar teeth, and others with flat-crowned molars. The former he placed in the Order Cynodontia, and for the latter he made a new Order, the Gomphodontia. Fortunately he was able to describe much of the postcranial skeleton of both types. The skeletons were shown to be in many characters very mammal-like, but even more remarkable was the discovery that these higher types have a secondary palate like the mammals and a much reduced quadrate. Notwithstanding, however, these very mammal-like characters SEELEY inclined to the view that these Cynodonts and Gomphodonts were not ancestral to the Mammals or even nearly related to them, but had acquired mammal-like characters by a parallel development. SEELEY's most important work on the South African reptiles was published between 1889 and 1895.

In 1897 I came to South Africa to make a further study of the fossil reptiles and to see if I could solve the problem of the Origin of Mammals, but it was not till 1900 that I was able to do any collecting. In the last 25 years, however, I have been able to explore portions of all horizons, and with the assistance of such famous collectors as Mr. ALFRED BROWN, the Rev. J. H. WHAITS, Mr. W. A. VAN DER BYL and others, I have been able not only to add a very large number of new genera and species to those previously known, but to do something towards a clearer understanding of the structure of the various types. In 1903 I showed that the mammal-like reptiles of the lower beds differ from the Cynodonts of the upper beds in having a Rhynchocephalian type of palate, with no trace of a secondary palate, and I placed these early types in a new Order, the Therocephalia. In the course of time it was seen that there were other carnivorous types that could not be placed in either the Cynodontia or the Therocephalia. Some of these were in 1913 placed in the Order Gorgonopsia, of SEELEY.

In 1911 D. M. S. WATSON first became keenly interested in the South African fossil reptiles. Bringing to the subject a rare enthusiasm and an expert knowledge of comparative anatomy he was soon able to add much new light to the subject. By spending six months in South Africa in 1911 he obtained an intimate acquaintance with the rocks and their fossils, and in the last fifteen years he has published many papers dealing with his South African finds, and he has worked out much more fully than had previously been done many of the treasures in the British Museum.

Since 1910 S. H. HAUGHTON has been associated with the South African Museum and has added considerably to our knowledge of the carnivorous mammal-like reptiles; while Dr. E. C. N. VAN HOEPEN, formerly of Pretoria but now of the Bloemfontein Museum, has given preliminary descriptions of one or two very interesting new types.

In the present state of our knowledge we have for convenience been dividing the carnivorous mammal-like reptiles into the Therocephalia, the Cynodontia, the Bauriamorpha, and the Gorgonopsia. The Therocephalia are those forms with simple uncusped molars, a narrow parietal region and a Rhynchocephalian palate. The Cynodonts are the higher forms with a narrow parietal region, cusped molars, and a secondary palate. The Bauriamorpha are a higher type with a secondary palate of a different type and uncusped molars. The Gorgonopsia resemble the Therocephalia in dentition and many other characters, but have a peculiar broad parietal region and a palate which though open is of a different type.

Unfortunately this simple classification is not quite satisfactory, as some new types have been found that cannot easily be placed in these groups, and others that, being of an intermediate structure, tend to break down the sharp distinctions of the groups. In fact no classification is likely to be completely satisfactory till our knowledge is greatly increased, not only as regards the many different carnivorous types that have lived, but also as regards the details of the anatomy of those already known. When one considers how many different classifications have in the last hundred years been given of the living mammals, in which every detail of the structure and development can be studied, one will not too hastily criticise the palæontologist who can usually study only fragmentary skulls, teeth and bones.

Our knowledge of the structure of the Cynodonts is fairly satisfactory, only a few points remaining unknown, but the Bauriamorphs, apart from the skulls, are very imperfectly known. Of the Therocephalians also our knowledge is still rather incomplete. We know many skulls, one or two pretty fully, but the postcranial skeleton is imperfectly known. Of the Gorgonopsians we know much of the skull, but apart from a nearly complete but rather badly preserved skeleton figured by AMALITZKY and PRAVOSLAVLEV, very little has been learned of the skeleton. In the present paper I shall fortunately be able to fill in nearly all the blanks in our knowledge of the Gorgonopsian structure. Before, however, dealing with the anatomy it may be well to review the work that has previously been done on this group.

In 1876 OWEN described, under the name *Gorgonops torvus*, the fairly complete skull of a moderate-sized Theriodont. He believed that the temporal region was completely roofed and that the skull also differed from the other known Theriodonts in the structure of the nostrils, and he placed *Gorgonops* in a group by itself, which he called the Tectinarialia.

LYDEKKER, in 1890, briefly redescribed the skull and agreed with OWEN in considering the temporal region to be roofed. "In the roofing of the temporal fossa," he says, "*Gorgonops* agrees with *Chilonyx*," and adds "This genus probably forms a connecting-link between the typical Theriodontia and the Pariasauria." He places it in the family "Gorgonopsidæ" but does not further determine its affinities.

In 1895 SEELEY also, agreeing with OWEN and LYDEKKER that the temporal fossa is roofed, placed it in a new Order, the Gorgonopsia. Something might be said in favour of retaining OWEN'S name Tectinarialia for the order, but as the peculiar condition of the nostrils is not a real character, but due to crushing, it seems better to accept SEELEY'S name, and as no one for many years has ever used OWEN'S term, while every recent worker has either used the ordinal term Gorgonopsia or the family name Gorgonopsidæ, it seems wisest to continue the use of these terms. In 1909 I carefully examined the British Museum type and found clear evidence that, though the parietal region is fairly wide, the fossa is not completely roofed.

In 1912 the Rev. J. H. WHAITS, perhaps the best fossil hunter South Africa has yet had, discovered at Beaufort West a practically complete skull of *Gorgonops torvus*, and a number of imperfect skulls of a nearly allied form, which I named *Scymnognathus whaitsi*. In the same year Haughton found two good skulls of allied forms at Dunedin. With these skulls I was able to show in 1913 that *Gorgonops* and its allies differ considerably from the typical Therocephalians and ought to be placed in a separate suborder, for which I revived SEELEY'S name Gorgonopsia.

The main points in which the Gorgonopsians seemed to differ from the Therocephalians were (1) the parietal region very broad, (2) the presence of a preparietal bone, (3) a large postfrontal bone, (4) a very large postorbital which forms the whole of the upper temporal margin, and meets the squamosal, (5) the absence of a suborbital vacuity in the palate, and (6) the mandibles united by a powerful symphysis. Two other differential characters were given, which later research showed to be in error.

At the same time as I was studying the Gorgonopsians in South Africa, WATSON, in London, was making a study of *Gorgonops*, and the much-weathered but excellent posterior half of the skull of another small type, which he found in the British Museum collection. He arrived at conclusions not very dissimilar to those to which I was led. In 1914 in a second paper—" Notes on some Carnivorous Therapsids "—he figured the occiput, and gave some account of the brain-case. He also discussed the relationships of the Gorgonopsians with the Therocephalia, the Cynodonts and the Bauridæ.

In 1921 WATSON published an important paper : " The Bases of Classification of the Theriodontia." In this paper he described at length the imperfect skull of *Arctops willistoni*, the type skull of *Gorgonops torvus*, a fairly good skull of *Scymnognathus whaitsi*, a new type which he described as *Leptotrachelus eupachygnathus*, the types of *Lycosaurus pardalis* and of *Arctognathus curvimola*, and a small Aelurosaurid skull in the British Museum. He also gave a restoration of the skull of *Rhopalodon fischeri*. From this wealth of material he was able to give most of the details of the structure of the skull, and even to discuss the trends of evolution in the group.

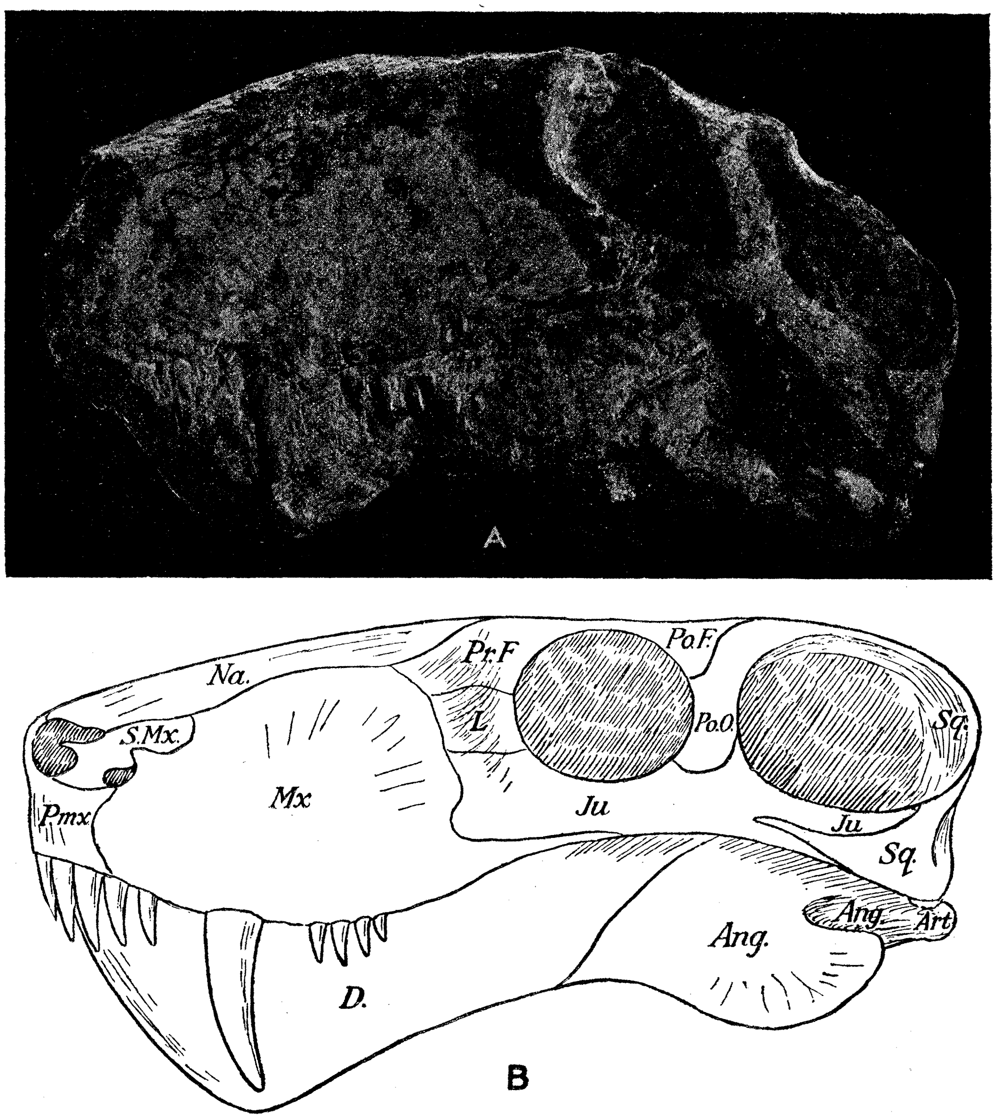
There is one point in WATSON'S paper which one can hardly allow to pass without a word of congratulation to him on his insight. He says (p. 77) :—" It will appear from the evidence to be brought forward in this paper that the forms from Dunedin and Nieuwveld localities are early, those from New Bethesda and the Kagaberg, which are associated with *Dicynodon tigriceps*, considerably later in time. There is, however, no stratigraphical evidence that this is so." We now know that Dunedin is a lower *Endothiodon* zone locality. New Bethesda is almost certainly in the *Cistecephalus* zone, while we know for certain that *Dicynodon tigriceps* is from the base of the *Cistecephalus* zone. Dunedin is thus probably 800 to 1,000 feet lower geologically than New Bethesda. The only points in the Gorgonopsian skull that WATSON leaves in doubt are the nature of the basicranial axis, the median bony septum and the structure of the pterygoid and epipterygoid.

HAUGHTON, in addition to his having described the oldest known Gorgonopsian, *Galesuchus gracilis*, added greatly to our knowledge of the higher types. In 1918 he described a very large form under the name *Gorgonognathus longifrons*, and in 1923 he published an important paper "On Some Gorgonopsian Skulls in the Collection of the South African Museum." He gives in this paper some further details of the structure of *Galesuchus gracilis*, *Scylacops capensis*, *Aelurognathus tigriceps*, and *Aelurognathus serratidens*, with a number of new figures. He gives figures of the skull of *Gorgonognathus longiceps* and shows the detailed structure of the palate. Of a new species, *Arctognathus whaitsi*, he is also able to give a good drawing of the palate. An important new genus and species is named *Sycosaurus laticeps* and three views are given of its skull, including one of the nearly perfect palate. A figure of a good palate of an unnamed form is also given and some sections through the median plate illustrated. Recently HAUGHTON has described two new Gorgonopsians from Nyassaland which agree closely with Karroo forms.

In 1927 two extremely important papers by P. A. PRAVOSLAVLEV were published in Leningrad, giving for the first time full descriptions of the Dwina Gorgonopsians. Over 20 years ago AMALITZKY distributed photographs of the skull and skeleton of *Inostranevia alexandri*, but so far as I am aware no descriptions were published. PRAVOSLAVLEV now publishes in his first paper full descriptions, not only of *Inostranevia alexandri* but a number of other species, and of a new species *Amalitzkia vladimiri*. The skeleton of *Inostranevia alexandri* is complete, except that the ribs, sternal apparatus, hands and feet and distal portion of the tail are missing. The skull is shown to agree very closely with that of many of the South African types, especially the larger forms such as *Scymnognathus*. The agreement is so close that one can safely assume that they belong to the same family, and although in most of the specimens the cranial sutures are not distinct, we may be moderately certain that they are as in the better preserved South African forms. From the photographs issued originally by AMALITZKY and reproduced by PRAVOSLAVLEV, the number of pre-sacral vertebræ appears to be twenty-six, though PRAVOSLAVLEV is apparently doubtful of the exact number. He states, however, that there are four sacral vertebræ. *Amalitzkia* is an allied genus, interesting in having four intervertebræ between the four vertebræ following the axis.

The Skeleton of Lycænops ornatus, BROOM.

The beautiful Gorgonopsian skeleton which forms the type of *Lycænops ornatus* was discovered by me in 1920, by the side of the railway line, about two miles south of Biesjespoort railway station. It lay on a slope of shale, which is weathering so fast that on revisiting the spot two years later it was with great difficulty that the exact spot could be identified. When first discovered only the front end of the pubis was exposed and a part of the femur, but on digging into the shale nearly the whole skeleton was found, for the most part lying as the animal had probably died. Most of the cervical region and most of the tail had been weathered away. A few phalanges and carpal bones of one hand, and some phalanges of the other and of both feet were not discovered, and some parts of the shoulder girdle are missing and probably were removed before the skeleton was covered by mud, but otherwise the skeleton is practically perfect. As is the case with all Karroo fossils there is some degree of crushing, but most of the bones except the vertebræ are beautifully preserved. Fig. 1, Plate (27) shows the skeleton as it lay in the shale. Figs. 2, 3 and 4 are the undersides of the skull, shoulder and pelvic regions.



TEXT-FIG. 1.—Skull of *Lycœnops ornatus*, BROOM. About ½ nat. size. A, as preserved; B, outline with distortion corrected.

The skull is in excellent condition. The left temporal region is somewhat crushed downwards, and the right temporal region is much crushed forwards, but it is not difficult to give views of the skull as it would be in the uncrushed condition. Text-fig. 1 shows the side view of the skull, and fig. 27, Plate (29) the top view.

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The maxillary bone is moderately deep, on its upper side it meets the nasal and the septomaxillary and there is a large oval foramen between the septomaxillary and the bone. There are one large canine and four molars, all of which are long and slender, and there are apparently no serrations either on the front or posterior edges of the teeth. There are five incisors and these also are long, rounded, pointed teeth, though possibly there may be serrations on the posterior edge on some. The figure shows the shape of the bones on the side of the face. The lacrymal is irregularly quadrangular; the jugal has a very large anterior facial portion and behind clasps the anterior process of the squamosal, also sending a short process up behind the postorbital. The squamosal has a very sharp slender posttemporal edge, and its lower anterior process is apparently quite slender, as is shown in the drawing.

On the upper side of the skull all the sutures can satisfactorily be made out. Most of the bones are considerably pitted. The preparietal is unusually large and is as broad in front as behind. The frontals are long and pointed in front, and they form a small part of the orbital margin. The pineal foramen is small and in the middle of a little raised boss. The parietals are small.

The occiput is very similar to that of other known Gorgonopsians, and especially in *Scylacops*. When *Scylacops* was first described the tabular was supposed to be a portion of the squamosal. Later this error was discovered, and HAUGHTON has given a good figure of the occiput of that genus. The interparietal is a large broad bone situated between the parietal and supraoccipital, and entirely on the occipital face. Below it lies the large broad supraoccipital, which forms the upper margin of the foramen magnum and the inner margin of the lateral occipital foramen. It articulates inferiorly with the exoccipital and the opisthotic. The tabular forms the outer portion of the occiput. Above it articulates with the parietal and the squamosal, and inferiorly it sends down a long process, which lies against the squamosal externally and the opisthotic internally and possibly has a part in articulation with the quadrate. The exoccipitals are quite small and form the lateral walls of the foramen magnum, articulating above with the supraoccipital and below with the basioccipital, although one cannot clearly make out the sutures with the basioccipital. The foramen for the IX, X and XI nerves lies between the exoccipital and the opisthotic on the outer side of the occipital condyle. Much careful preparation will be required before it will be possible to give a full account of the palate, but so far as can be seen it agrees closely with that of other known Gorgonopsians.

The lower jaw is considerably crushed. In front it is deep and rather massive between the upper canines. Posteriorly, as far as can be seen, it agrees closely with that of other Gorgonopsians.

The cervical vertebræ are mostly lost, but one of the halves of the atlas-arch is preserved, and the lower portion of the atlas. The atlas arch agrees closely with that of other known Therapsidans. It is interesting to observe that the two sides of the arch have been separated. In the Cynodonts they are united as in mammals, and in the Titanosuchids they are also united, while in the Tapinocephalids they are separate

They are also separate in the Anomodonts. In the Therocephalians the condition is unknown. The lower part of the atlas is interesting from the evidence it shows of there having been attached to it on each side a small rib, as in the crocodile.

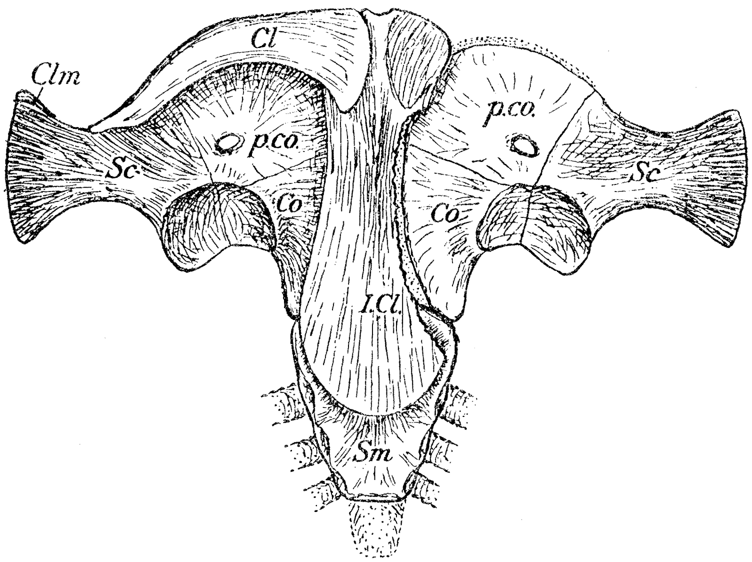
From apparently the eighth vertebra the series is continuous to the sacrum, but most of them are considerably crushed. Very careful preparation will be required before the full details of the vertebræ can be made out. There is only slight evidence of one or two intercentra, but possibly very feebly developed intercentra may have been present between all the vertebræ. All the centra are narrow and considerably constricted and the ends appear to be only very slightly concave. The transverse processes are well developed, but the spines in at least the more posterior vertebræ are relatively short. There are twenty pre-sacral vertebræ preserved apart from the missing cervicals, and it seems probable that the whole number was twenty-seven. The sacrum has two vertebræ preserved, and it is probable that there were three. The first has a very large costal element, which has a deep articulation with the ilium. The second has a relatively small articulation and so probably had the third. The sacral vertebræ are not completely fused to each other.

Although the cervicals are lost in this specimen, fortunately they are well preserved in the type of *Aelurognathus tigriceps*. Here there are seen to be a well developed pro-atlas on each side resting on the upper arch of the atlas, as shown in the figure, and the atlas has a rib springing from each side. The axis is formed as in other known Therapsids. The odontoid element is relatively small and there is a large intercentrum between it and the body of the axis. The third, fourth, fifth, sixth and seventh cervicals have transverse processes, which increase in size on passing backwards, as shown in the figure.

The shoulder girdle is not very well preserved. The lower portion of the scapula is expanded to give articulation to the large flattened precoracoid of the upper part of the coracoid. As shown in the figure the precoracoid is irregularly quadrangular, though rounded in front. Its posterior edge just enters the glenoid cavity. The coracoid is rather small and crescent-shaped. The articular surface looks entirely outwards. The clavicles, though preserved, are somewhat crushed, and there are small portions of the interclavicles also preserved.

The most interesting point in connection with the shoulder girdle of this specimen is the fact that there is a large well-developed ossified sternum. In the plate this is figured in the crushed condition, and in the text-fig. 2 as it would appear before being crushed. There is little doubt that its upper border articulated with the coracoid and its lower border has a clear articulation for either a cartilaginous or bony xiphisternum. On the sides there are the articulations for certainly three ribs, and I think possibly for four.

Both humeri are nearly perfectly preserved and they are of the type long since described by Owen in *Cynodraco serridens*, Ow. With careful preparation most of the muscular attachments will, I believe, be revealed. In the meantime it seems but necessary to state that they are relatively large in comparison with the size of the skull. In marked contradistinction to the condition in *Cynognathus* the radius and ulna are also long and moderately slender and only slightly shorter than the humerus. The ulna is remarkable in being much flattened and there is a well developed olecranon process.



TEXT-FIG. 2.—Front view of shoulder girdle of *Aelurognathus tigriceps*, BR. and HTN. About ½ nat. size. *Cl.*, clavicle; *Clm.*, cleithrum; *Co.*, coracoid; *I. Cl.*, interclavicle; *p. co.*, precoracoid; *Sc.*, scapula; *Sm.*, sternum. (Restored.)

The carpus is completely preserved. Proximally there is a short, rather rounded radiale, a long, somewhat flattened ulnare with a very small narrow intermedium between them, and outside of the ulnare is a well developed pisiform. Below the intermedium is a small centrale. Distal to the radiale is a radial central. There are four distal carpal elements, the first and second being comparatively small, the third moderately large and the fourth still larger.

In the specimen as found the metacarpals have been dislocated from the carpus in the left manus, but they are in undisturbed relative position. The first digit is represented by a short metacarpal, a short first phalanx and an ungual distal phalanx. The second digit has a longer metacarpal, two well developed phalanges and a distal ungual phalanx. The third digit has a longer metacarpal than the second, a well developed first phalanx, then a very much flattened second phalanx, a well developed third phalanx doubtless followed by the claw phalanx. The fourth digit has a much longer metacarpal than the third, a well developed first phalanx, followed by two very short phalanges, then a short, almost square phalanx which was doubtless followed by the claw phalanx. The fifth toe is entirely missing.

The pelvis is almost perfectly preserved on both sides. The ilium is short and broad, and the acetabular portion occupies about a third of the whole bone. In front the crest only passes a very short distance in advance of the acetabulum, and the posterior portion

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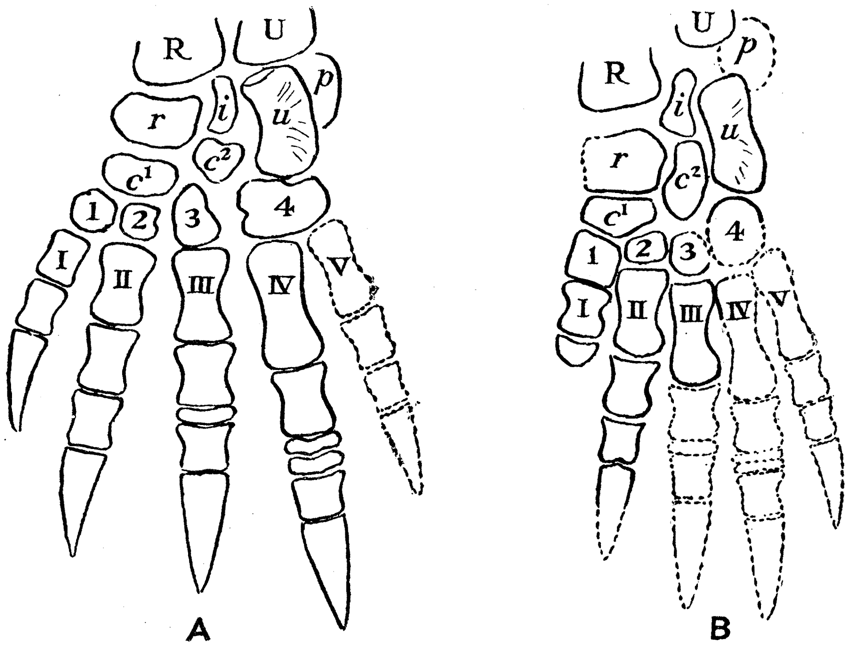
only a very little distance behind the articulation of the ischium. The shape of the bone will be best understood from the figures given. The pubes are moderately flat and there is a large pubic foramen, apparently completely surrounded by bone. The lower portion of the pubis is very thin, though probably it was thicker along the symphysis. The upper margin of the pubis is relatively strong.



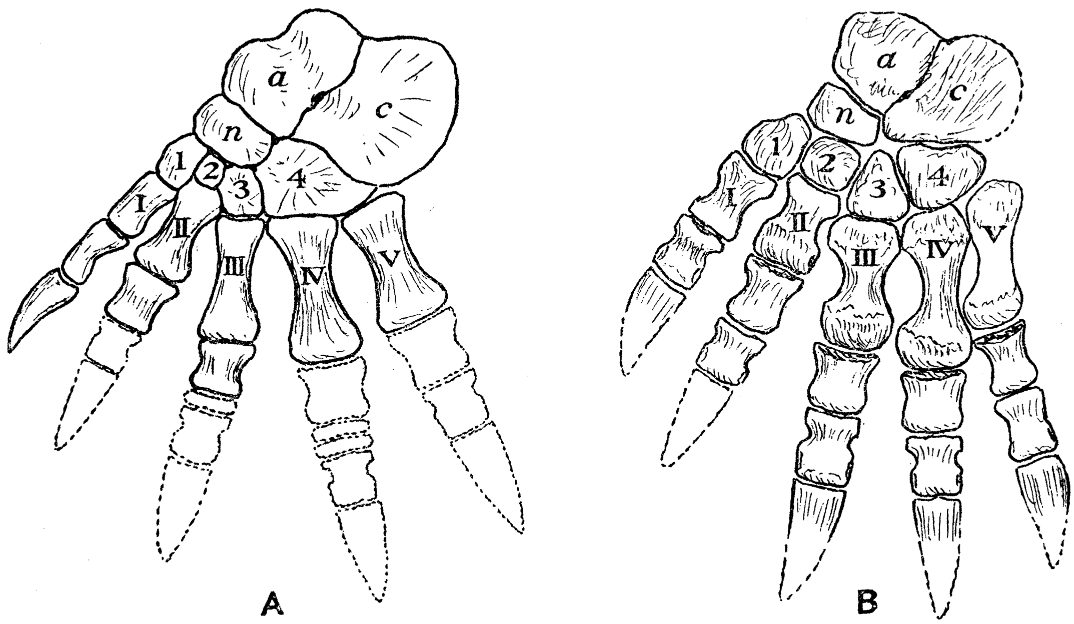
TEXT-FIG. 3.—A, left manus of *Lycænops ornatus*, BROOM. About $\frac{1}{2}$ nat. size. B, left manus of *Cynognathus crateronotus*, SEELEY, or a nearly allied carnivorous Cynodont. About $\frac{1}{2}$ nat. size. c^1 c^2, the two centralia; *i*, the intermedium; *p*, the pisiform; *r*, radiale; *R*, radius; *u*, ulnare; *U*, ulna; 1, 2, 3, 4, distalcarpals; I, II, III, IV, metacarpals.

The ischium is deep, though relatively short. It and the pubis are both only slight modifications of the plate-like type. The lower portion of the ischium is relatively thin and extends back to a moderately well developed posterior ischial tuberosity. The whole pelvis will be seen to resemble considerably that of the Pelycosaurs and to differ very markedly from that of the Cynodonts and Anomodonts. It also differs considerably from the pelvis of the Dinocephalians and agrees fairly with that of the Dromasaurians. The pelvis is not at present fully known in any Therocephalian, but we know the pubis and ischium in at least two genera, and these agree closely with those of this Gorgonopsian.

The femur is long and rather robustly developed. It resembles the femur already known in *Aelurosaurus*. The great trochanter is only slightly developed, with a small second trochanter. There is apparently no ossified patella. The tibia is long and rather slender, and the fibula quite thin, except at its upper end, where it is broadly expanded to articulate with the femur, and at its lower end where it articulates with the calcaneum.

The tarsus is perfectly preserved on the left side, and fairly well preserved on the right, though the elements are separated. There is a large rounded astragalus and a large, flattened rounded calcaneum. In front of the astragalus is a short navicular, and there are four distal tarsal elements, as are shown in the text-fig. 4.

In the specimens as preserved the hallux is folded around on the sole of the foot, but in text-fig. 4 is shown as it probably originally lay. The first distal tarsal is a small



TEXT-FIG. 4.—A, left pes of *Lycænops ornatus*, BROOM. About $\frac{2}{3}$ nat. size. B, left pes of the Upper Cistecephalus zone Therocephalian *Whaitsia platyceps*, HTN.—for comparison. About $\frac{2}{3}$ nat. size. *a*, astragalus; *c*, calcaneum; *n*, navicular; 1, 2, 3, 4, distal tarsals; I, II, III, IV, V, metatarsals.

rounded element, the second is considerably smaller, the third slightly larger but narrow, and the fourth quite a large element, which articulates with the third tarsal, the navicular, the calcaneum, and the fourth and fifth metatarsals and possibly the astragalus. The first metatarsal is short and broad, its first phalanx also short and rather feebly developed, and the ungual phalanx long and narrow. The second, third, and fourth metatarsals steadily increase in size and they are all relatively narrow. The fifth is shorter than the fourth and much broader. Only two phalanges are preserved, the first phalanges of the second and third toes, and these are relatively small. It seems probable that a considerable pad lay underneath the calcaneum and the astragalus, and that the animal was plantigrade. It may have walked with most of the weight of the foot on the os calcis pad and on the fourth and fifth digits.

Descriptions of Sections Through the Skull of a Young Gorgonopsian.

I discovered near Biesjespoort some years ago the skull of a beautiful little Gorgonopsian in a lime nodule. It was quite manifestly an immature specimen, and

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thinking it probably represented a young specimen of *Cynariops robustus*, Broom, I had it cut in as large a series of sections as was practicable, by Mr. Lomax, of Bolton. The specimen has been most beautifully cut, and the sections reveal in every detail the internal structure, excepting in the occipital region where the elements are somewhat displaced by crushing. I have, however, come to the conclusion that the specimen represents a distinct species, which I propose to name *Cynarioides gracilis*. The figure given in Plate (30), fig. 28, shows an upper view of the skull of natural size, and indicates as near as can be determined the position on the skull of each of the sections figured. Each slice has of course two sides, so that while only 35 are here figured, there are really 72 sections for study.

Section I.—The tip of the snout is missing and with it the front of the premaxillary bone and most of the septomaxillaries, so that no account can be given of this part. The first section which I figure is through the premaxillary bone and shows in section the tips of the first and second upper incisors, the roots in the bone of the third incisors and internally the roots of the second replacing incisors and a portion of the root of the first replacing incisor.

Section II.—This section shows the third incisors cut across, the roots of the fourth incisors, a small portion of one of the second incisors and the tips of the four lower incisors. All these are of the first set. Lying inside the third upper incisors are the germs of the third replacing incisors. The two premaxillaries are meeting each other in the middle line and forming a palatine process. Above the inner parts of these premaxillaries is seen the anterior end of the prevomer.

Section III.—Section III represents a section through the posterior part of the premaxilla where it is overlapped by the anterior part of the maxilla. Above is seen a portion of the nasals. In the premaxillæ are seen the roots of the fifth incisors and internal to them are the germs of the replacing incisors. Below the bones are the fourth incisors cut across; then in the middle of the section is seen the median prevomer clasped at its base by the palatine processes of the premaxillæ. The anterior ends of the dentaries are seen in the lower part of the section. Three incisors are seen cut in section on each side. These are the first, second and third incisors of the first set, and above the first on each side are seen the tips of the germs of the first replacing incisors.

Section IV.—In this section the snout consists only of the two maxillæ and the two nasals with the median prevomer. The prevomer has its lower part in the form of two brackets which doubtless held the organs of Jacobson. Below the maxillæ are seen in section portions of the fifth incisors of the first set. In the sections of the mandible are seen on the left side the four incisors of the first set cut across and the tip of the third replacing one. On the right side is seen a section of the second replacing one.

Section V.—The nasals and maxillæ are very similar to those in the previous section, but the prevomer is seen in two portions owing to the large fenestra that occurs in the bone. In the lower jaw are seen the two large canines in section. On the left side are seen cut across the roots of the four incisors and the cavities for the germs of the third and fourth replacing incisors. On the right side are seen the bases of the first and fourth incisors.

Section VI.—The maxillæ show the parts of the alveoli for the large functional canines. The prevomer is still seen in two parts. The upper doubtless is grooved for the reception of the base of the median septal cartilage. The lower part is no longer bracket-shaped, clearly indicating that the Jacobson's organ was a round short organ as in *Ornithorhynchus*, rather than an elongated one as is generally found in mammals. The mandibles each show the lower part of the functional canines cut across. On the right side is seen the base of what is manifestly the replacing canine, and inside of it there is the tip of a third replacing tooth. The tip is inverted, pretty certainly *post mortem*. On the left side is seen lying on the inside of the canine the tip of the replacing canine.

Section VII.—Here the maxillæ are of large size and show the functional canines cut almost longitudinally. The prevomer is very similar to that in the previous section. The mandibles show the bases of the functional canines and sections of the replacing canines. From the last three sections it is manifest that while there is only evidence of two sets of incisors, there is clear evidence of at least three sets of canines.

Section VIII.—In Section No. VIII the maxillæ are of large size and present a most complicated arrangement of teeth. On the right side are seen portions of three canines. By the side of the mandible is the tip of the functional canine and at the very top of the maxilla the base of the root of the functional canine. To the outer side of the bone is a portion of a canine surrounded by bone and with bone appearing in its pulp cavity. This is the remains of a canine earlier than the one now functional. On the inner side of this right maxilla is the third developing canine and still more internal is the cavity for the germ of the fourth canine. On the left side near the middle of the bone is seen a section of the functional canine, and outside of it, completely surrounded by bone, the remains of an earlier canine. Inside the base of the functional canine is seen a section of developing third canine and in the cavity more internal is the germ of the fourth canine inverted. The mandible on the left side shows the base of the functional canine. There is also seen the anterior portion of the splenial. On the right side is seen the first molar in section.

Section IX.—Here the maxillæ still show a most complicated arrangement of teeth. On the right side are seen a little portion of the base of the functional canine, a large section of a developing replacing canine, and the cavity for the germ of the fourth canine. At the alveolar margin of the bone is seen the base of the first molar. On the left side there is seen a section of the replacing third canine, and on the inner side of the bone there is in a cavity the tip of a small developing tooth. This can hardly be the same tooth as is seen in Section VIII. The enamel there appears inverted while here it is in the right position. We seem forced to conclude that we have here another developing canine. The prevomer has its upper and lower portions now united, the section being behind the large fenestra. In the lower jaw is seen on the right side a molar in section, probably the third, and at its base a large section of the splenial. On the left side is seen a section of a molar and also a large section of the splenial. In this section there is seen the anterior tip of the lacrymal bone at the base of the outer portions of the nasals.

Section X.—On the right side the maxilla shows a large antrum with an opening into the nasal cavity above. There is seen inside the maxilla the anterior part of the palatine, and between the maxilla and the nasal lie two portions of the lacrymal, the lacrymal duct having lain between those two portions. On the left side the lacrymal bone is seen surrounding the duct. This section shows that that lacrymal bone passes much further forward than would appear from the part showing on the facial surface. The prevomer is seen forming a median keel with its upper portions clasped by the palatines. This section is just behind the posterior nares, and the palatines are here forming the posterior walls of the nares. The lower jaws show sections of two molars, probably the second. There are also seen sections of the splenials.

Section XI.—Here the inner and outer parts of the palatines are completely joined. The inner portions still clasp the prevomer. The nasal passages lie below the deep hollows of the palatines, and doubtless a false palate passed from the palatine of one side to that of the other. The maxillæ show on each side molars in section, two on the right probably third and fourth, and one on the left, probably the third. In the lower jaws there are seen two molars in section, probably the fourth.

Section XII.—The palatine on the right side is slightly broken by crushing; the two still clasp the prevomer. Each maxilla shows a molar in section, probably in each case the fifth. The lacrymals are large and now appear on the face, the lacrymal canal being seen in the centre of each bone. In the upper part of the section are seen in section the frontal and prefrontal bones. In the lower jaw are seen in section on each side the dentary on the outside, the splenial on the inside, and the anterior part of the angular between them. In the various sections that we have examined there is no clear trace of any replacing molars.

Section XIII.—The palatines are seen as fairly strong bones, but this is in part due to the bone being somewhat curved and cut obliquely. The inner ends still clasp the posterior tip of the prevomer and above the prevomer lies a median bone which is the anterior end of the united pterygoids. The lower jaw in section shows on each side a new element. Externally is the powerful dentary, internally the slender posterior part of the splenial, and between them the angular, while on the inside of the upper part of the dentaries are seen the anterior ends of the prearticulars.

Section XIV.—Here the palatines unite in the middle line and the prevomer is no longer seen. Between the palatines and above their inner ends is seen the median united pterygoids. In the upper part of the section are seen the frontals, outside of them the prefrontals, and below these the lacrymals still showing the duct. Below the lacrymals are seen the jugals and below the jugals the posterior ends of the maxillæ. The mandibles show the elements as in the previous section.

Section XV.—The two palatines are here separated in the middle line by the united pterygoids, which still form a thin ascending median plate. There is between the two palatines a median deep channel which probably held the nasal passages, probably still separated from the mouth cavity by a false palate. In the middle part of the section there is seen the anterior tip of the developing presphenoid. On the left side the section passes through the anterior part of the orbit and shows the prefrontal in two portions. Below the lower is a section of the lacrymal. This contains a duct and on the other side a deep groove, which can be seen by the adjoining section to be also for the lacrymal duct, clearly indicating that in the Gorgonopsians there are two lacrymal openings as in the Marsupials. On the right side the two ducts are seen united together. On the right side in the section of the lower jaw are seen the posterior tip of the splenial in section, the prearticular cut across, and above the inner part of the angular the anterior tip of the surangular. On the left side is seen the anterior tip of the coronoid.

Section XVI.—Section XVI is through the anterior part of the orbits of both sides, above which show the frontals with the prefrontals on their outer sides, and below the frontals the median presphenoid with its orbitosphenoidal wings. Here manifestly these orbitosphenoidal wings are parts of the presphenoid bone. Below the orbits on each side are seen large sections of the jugals, and below the jugals the posterior tips of the maxillæ. The median pterygoids still form a slender median plate and now a broad basal portion. Part of the right side of this section is here crushed. The palatines in this section bear teeth ; on each side three are cut across. On the outer sides of each palatine are seen the anterior tips of the transpalatines. The lower jaws show the dentaries still large, with the angulars below, and on the inner sides of the dentaries, in the cavities, the tips of the surangulars. On the inner sides of the upper part of the dentaries are seen on each side two bones, the lower is the prearticular and the upper the coronoid.

Section XVII.—This section is still nearer the middle of the orbits. By the sides of the frontals are seen the posterior tips of the prefrontals and below the frontals the moderately large presphenoid with the orbitosphenoidal wings passing upwards and outwards. On the right side is an opening at the base, which is probably for the optic nerve. The jugals are still large in section. On the left side are still seen the posterior tip of the maxilla, the transpalatine and the palatine. In the middle line the united pterygoids still form a thin median plate, which is cleft in front as if to receive the base of the presphenoid cartilage. On the right side the transpalatine has a large foramen. The lower jaw on the right side shows the dentary no longer forming the base of the jaw, with the angular forming the base, and the coronoid, prearticular, and surangular as in the previous sections.

Section XVIII.—In the region of Section XVIII the skull had been first cut in two, rather unskilfully by myself, and the sections of the anterior and posterior halves had been independently made so that in this region the sections are not quite complete, and the posterior ones lack the upper portions of the skull, as the preparietal region was sectioned off and preserved as a specimen. The presphenoid is still seen and the upper part of the skull is probably as restored. In the lower part of the section the palatines are now lost, though the section cuts through the suture between them and the pterygoids. Portions of both transpalatines are seen. The lower jaws are not satisfactorily seen on either side, but there is no difficulty in identifying the elements by comparison with the previous sections.

Section XIX.—This section shows the pterygoids with teeth. The pterygoids are still united in the middle line. On the left side a large portion of the transpalatine is still seen. The lower jaw on the right side shows the dentary, angular, prearticular, coronoid, and surangular.

Section XX.—Here the pterygoids are now apart and the transpalatine no longer seen. Two teeth are still seen on the inner part of the bones. The lower jaws are not perfectly preserved, but show the prearticular, coronoid, surangular, dentary, and angular bones.

Section XXI.—Section XXI shows the pterygoids as large flat bones still separate in middle line. The mandibles, though slightly imperfect, still show the same elements as in the previous sections.

Section XXII.—Section XXII is through the posterior part of the broad palatal portion of the pterygoids. They are still fairly widely separated in middle line. The sections pass through the transverse dental region and teeth are shown on each side. The lower jaw on the left side shows the large angular with the dentary above; on the inner side still the coronoid and the surangular above, and the prearticular below. By the side of the prearticular is a small bony element, which is the posterior lower process of the coronoid. On the right side the only elements showing are the large angular, with inside the surangular and the prearticular, and above the lower portion of the dentary.

Section XXIII.—Here the pterygoids show in two portions, the median portions having again approached each other, though they do not unite. The outer portions are the posterior tips of the broad palatal parts. The lower jaw on the left side shows the large angular, a small portion of the dentary and inside of the angular are sections of the surangular and prearticular. On the right side the very large angular, surangular and prearticular are shown.

Section XXIV.—Here a new element is seen. Between the pterygoids a median plate appears and above in the middle line is a grooved vomerine-like element. These two median bones are parts of the element which most authors regard as the parasphenoid, but which in my opinion is homologous with the mammalian vomer. Though the upper vomerine-like process does not appear in any of the more anterior sections, the transverse slice which removed the upper surface of the skull shows that it ran forward a considerable distance further. The lower jaw on the left side still shows the large angular, with inside it the surangular and prearticular, and above the coronoid process of the dentary. On the right side are similar elements, but without the coronoid process.

Section XXV.—The median elements here are seen to be in an interesting condition. The upper vomerine-like process is approaching the lower, and while the upper has a grooved upper surface for the presphenoid cartilage, the lower element also has an upper grooved surface. This lower element, however, probably lodged, not cartilage, but a lymph gland. By the sides of the lower vomer are seen the pterygoids, hollowed out on the upper surface to clasp the anterior part of the bases of the epipterygoids. The lower jaw on the left side shows the large angular, split in its lower half into an inner and outer plate, and under its inner side are the prearticular and the angular. On the right side a similar condition is seen.

Section XXVI.—Here the upper and the lower anterior processes of the vomer or parasphenoid are united. By the sides the pterygoids are still seen clasping to some extent the bases of the epipterygoids. On the left side the large angular is seen as an outer and inner plate which are united above, and inside are the large surangular above and prearticular below. In all the Therapsids proper a similar peculiar condition of the angular exists, as I showed in my paper on the Dinocephalian skull, and even in the Pelycosaurs a somewhat similar condition, though less developed, is seen. What this large cavity at the posterior part of the angular was for is unknown, but it seems to me that it may have been for the holding probably of a very large salivary gland, perhaps the submaxillary. The lower border of the jaw inside of the cavity is always smooth and rounded.

Section XXVII.—Here the vomer or parasphenoid shows the large median keel with two lateral wings. Outside these wings are seen the posterior extensions of the pterygoids and resting on them the bases of the epipterygoids. The lower jaw on the left side shows the angular, with the outer plate now free, and on the inside the large surangular and prearticular.

Section XXVIII.—The vomer or parasphenoid is here a little narrower, but still shows the median keel and the lateral wings. The two posterior processes of the pterygoids are still seen in section, and the epipterygoids are seen cut almost longitudinally. The lower jaw is very similar to that seen in the previous section.

Section XXIX.—The vomer or parasphenoid is still narrower, owing to the less development of the lateral wings, but the median keel is still large. Above the bone in the middle line are seen the anterior parts of a new element. These are portions of the prootic of the right side slightly displaced. On the left side are seen the posterior process of the pterygoid with above still a portion of the epipterygoid. Above the epipterygoid is a small crescent-like element. This is the anterior end of the prootic of the left side. The lower jaw shows the inner plate of the angular, now very thin, and the outer plate detached from it and also very thin. The surangular and prearticular are quite powerful elements here. On the right side the lower jaw shows clasped by the prearticular the anterior part of the articular, and above this the surangular. Outside is the posterior end of the angular.

Section XXX.—Here the vomer or parasphenoid is rather stout and the median keel is much reduced. Above it lies the anterior portion of the prootic. On the right side are still sections of the epipterygoid and pterygoid, and the lower jaw on the right side shows a large articular, clasped below by the prearticular, externally by the angular, and above by the base of the surangular. On the left side the lower jaw shows sections of the surangular and prearticular, and the posterior end of the outer plate of the angular. Between the lower jaw and the vomer are still sections of the pterygoid and epipterygoid, and above these still a portion of the prootic of the left side.

Section XXXI.—Here a most interesting condition is seen. The vomer is very broad, with a median hollow between the two sides, and in the space above are what appear to be a pair of elements. These, however, on comparison with the anterior section are evidently the posterior continuations of ossifications of the vomer above. Inside, and above the vomer, are two elements which prove to be still portions of the prootic, and a portion of the other prootic is also seen. On each side are sections through the posterior parts of the pterygoids. Below the pterygoid on the right side is a small element which is the anterior border of the inner end of the stapes. Above this pterygoid is the posterior end of the epipterygoid. The section of the mandible on the left side shows the three membrane bones, the angular, the surangular and the prearticular, with the anterior end of the articular.

Section XXXII.—This section is very similar to the previous one. The two portions of the prootic lying above the vomer are here united. A larger portion of the inner end of the stapes is seen. To the right of the pterygoid on the right side is an element which cannot be identified with certainty. The bones in this region are considerably crushed and displaced. Possibly the element is part of the displaced quadrate.

Section XXXIII.—This section shows a number of interesting elements. On the left three portions of the squamosal are seen, which clasp the large quadrate and the small quadratojugal. The quadratojugal appears in two parts, probably due to fracture. The section of the mandible shows the articular with, on its outer side, the angular and on its inner and under sides portions of the prearticular. A large part of the prootic is still seen, with below it a section of the anterior end of the opisthotic. The anterior end of the basioccipital is seen cut across, with below it the large posterior expansion of the vomer. To the right of the basioccipital are sections of the prootic and opisthotic, and a beautiful transverse section of the stapes. As in the previous section the elements in this region are considerably crushed and displaced and cannot be identified with certainty, though there is still no difficulty in tracing the pterygoid.

Section XXXIV.—This section much resembles the previous one. The sections of the quadrate and the quadratojugal are interesting, being only very slightly displaced. The section of the mandible is very similar to the preceding one. Below the basioccipital are small portions of the posterior end of the vomer; and on each side sections of the prootics and opisthotics.

Section XXXV.—This section is only a short way from the foramen magnum. Above the basioccipital is seen the supraoccipital, and on each side sections of the opisthotic. A large section of the squamosal supports the fairly large quadrate, but the small quadratojugal is no longer present. The section is through the middle of the articulation of the mandible. Probably the whole section of the mandible is articular, except a thin plate below, which is probably prearticular, and a little element on the outer side which may be the posterior end of the angular.

Section XXVI.—This section shows part of the exoccipital and a large part of the left opisthotic. Inside the squamosal is what is probably a part of the tabular. Sections are still seen of the quadrate and articular, with what is probably still a part of the posterior end of the angular.

The Basicranial Axis and the Vomers.

Probably the most interesting result of the study of the skull of the Gorgonopsians is the light thrown on the mammalian basicranial axis and the origin of the mammalian vomer. Until recently it has always been assumed that in the mammalian skull there are four bones forming the basicranial axis, viz. :—the basioccipital, the basisphenoid, the presphenoid, and the mesethmoid. There are certainly these four in man, the dog, and the rabbit, the forms that have been most studied. In the reptiles, however, there are never more than three, of which the posterior two are certainly the basioccipital and the basisphenoid. But whether the anterior element, which is generally much in front of the basisphenoid, was to be regarded as the homologue of the mammalian mesethmoid or the presphenoid was a point that was difficult to settle. It was manifestly homologous with the so-called " sphenethmoid " of the frog, and for safety was generally referred to as the ethmoid or sphenethmoid. But if the mammal has always four bones, and even the higher Therapsids only three, how have the mammalian four arisen, and which of the four correspond to the reptilian three ? These questions puzzled me for some years.

One bitterly cold morning, about four years ago, I was called to attend a valuable cow in labour. The fœtal head was doubled back and the calf completely impacted. After working for about two hours I saved the cow's life, and I also saved what was to me more valuable, the calf's head. On examining the skull of this newly born calf I found to my surprise that there were only three bones in the basicranial axis, manifestly the basioccipital, the basisphenoid and the presphenoid. The mesethmoid region was still largely cartilaginous. Two points had to be settled :—Was the apparently single presphenoid really a single element, or would a mesethmoid develop later on ? The examination of earlier and later stages showed that at no period in development is there any mesethmoid bone, the whole mesethmoid region being ossified by the extension of the presphenoid. Flower and others have figured the large bone in the front of the axis, in the sheep and other ungulates, as a fusion of the mesethmoid and the presphenoid; but there is never really any trace of a mesethmoid.

It became at once necessary to look into the condition in other types of mammals, and fortunately I had in my own private collection a large series of skulls of young mammals, which soon revealed that many other mammals besides the Artiodactyles have only three bones in the basicranial axis. Of the few mammalian orders unrepresented in my collection I later found specimens in the British Museum and the American Museum, New York. I found that there are only three bones in the basicranial axes of Marsupials, Armadillos, Sloths, Artiodactyles, Perissodactyles, Elephants, Sirenians and *Chrysochloris*. There are four bones in the basicranial axes of *Manis*, *Procavia*, *Orycteropus*, Rodents, Insectivores, Carnivora, Pinnipedia, Menotyphla, Dermaptera, Chiroptera, Primates, and possibly Cetacea. In the whales I have not with certainty discovered a fourth element, but not improbably a rudimentary mesethmoid may occasionally be present; or possibly in some, with the reduction of the nasal structures, the mesethmoid may have been lost.

As in all known Therapsids there are only three bones in the axis, it seemed pretty manifest that the three would be likely to prove homologous with the three in the Artiodactyles, viz. :—the basioccipital, the basisphenoid, and the presphenoid; and that it is the mesethmoid that is the new element in the majority of mammals. But as in the Gorgonopsia the anterior element is very large and removed a considerable distance from the basisphenoid, the questions had to be very seriously considered whether this anterior element might not be the mesethmoid, with a potential presphenoid unossified, and whether, when only three elements are ossified, in some mammals a previously existing mesethmoid might not have been lost.

Fortunately in the American Museum I was able to examine the condition in the skull of a half-grown *Ornithorhynchus anatinus*. Dr. G. G. SIMPSON had dissected the skull in his study of the developing teeth, and the part he did not require was the very part I needed. A median section of this skull shows the very interesting condition which I here figure (Plate (34), fig. 38). The basioccipital and the basisphenoid agree fairly closely with those of Therapsids and mammals, but a third element lies far forward in the mesethmoid region. If one could examine only the median section one might suspect it to be the mesethmoid, and that the presphenoid is unossified, but an examination of the cranial wall shows that it supports the orbitosphenoids. From WATSON's figures it would appear that the orbitosphenoids have special centres of ossification.

There can thus be no question that it is the presphenoid, and in being well in front of the basisphenoid we have but a repetition of the exact condition we find in the Gorgonopsians, and we can thus conclude that in those lower mammals that have only three elements in the basicranial axis it is the mesethmoid that has never been developed. The median section of the skull of the young Platypus also shows a most interesting condition of the vomer, which will be referred to presently.

Until about 40 years ago everyone apparently accepted the view of CUVIER and OWEN that the homologue of the mammalian vomer was to be found in the pair of bones situated in the front of the palate in lizards and frogs; and the large median bone in the frog's palate, and the manifestly homologous spur in the lizard, required a new name and were called the "parasphenoid." In all text-books of this day these determinations are continued.

So far as I am aware the first to express any doubt on the correctness of these views was Bland Sutton, who in 1884 suggested that the reptilian parasphenoid was really the homologue of the mammalian vomer. In 1885 Smets independently supported this same view, but no other scientist looked with any favour on this heterodox view till ten years later when I was working at the comparative anatomy of the organ of Jacobson in reptiles and mammals. It seemed impossible to doubt that the organ of Jacobson in the lizard is homologous with the organ of Jacobson in *Ornithorhynchus*, and if this is so the cartilaginous capsules that support the organs must also be homologous. The capsules in each have on their inner sides supporting splint bones, and I was forced to the conclusion that these splint bones must also be homologous. But the splint bones in *Ornithorhynchus* unite to form the so-called "dumb-bell shaped bone," while the splint bones in the lizard become the so-called "vomers." As the "dumb-bell shaped bone" in *Ornithorhynchus* is not the vomer, which is well developed behind it, a new name became necessary and I proposed the name "prevomer" for it and for the "vomers" of the lizard which I regarded as homologous.

A few years later I endeavoured at greater length to trace out the homologies and in at least three instances, working with imperfectly known facts, was in error. The apparently single vomer-like bone in the Chelonians I regarded as a true vomer: I now regard it as the prevomer. The single median bone in the front of the palate of *Dicynodon* I also believed to be a true vomer. Later discoveries revealed that it is a prevomer, the true vomer lying above it. The vomer-like bone which supports the secondary palate in the Cynodonts was also regarded as a true vomer. Later facts revealed good reasons for considering this also as the prevomer.

The study of many skulls of Therocephalians and Gorgonopsians showed beyond doubt that the apparently single median bone in the front of the palate, lying between the internal nares, is really a pair of prevomers. In most Therocephalians the bones are fused, but in some smaller forms (*e.g.*, *Ictidognathus hemburyi*) the two bones remain distinct apparently throughout life. In all known Gorgonopsians, even when fairly young, the bones are fused. In most Therocephalians there is along each side a curved ledge for the lodgement of Jacobson's cartilage; so that transverse sections, as shown in the figure I give, are strikingly similar to sections across the "dumb-bell shaped bone" in *Ornithorhynchus*.

In the hinder part of the palate we usually have a median descending plate of bone, which has generally been regarded as a development of the basisphenoid. The young Gorgonopsian skull which I have described shows that this median plate of bone is part apparently of a membrane bone, which develops below the basisphenoid and passes even below part of the basioccipital. In front there is a slender spur that probably lay along the base of the median cartilage, and it would seem as if the cartilaginous basisphenoid is being invaded by the ossification of the membrane bone. A very similar condition occurs in many reptiles. There can be little doubt that this bone which forms the median descending plate in Gorgonopsians is the reptilian "parasphenoid," and if we knew of no other Therapsid palates we might well hesitate before regarding it as the mammalian vomer. Fortunately we get a very much more mammal-like condition in the Anomodonts.

In *Dicynodon* a median section reveals a most interesting condition. The basicranial bones are strikingly similar to those of a young Artiodactyle mammal, and in some respects even more similar to the condition in the young Platypus. The lower anterior border of the basisphenoid sends forward a long slender grooved process, which doubtless supported the median cartilage. When compared with the reptilian condition, as seen in an early reptile such as *Ichthyosaurus*, there can be no doubt that this anterior process is the "parasphenoid" of the reptile. But when a comparison is made with the condition seen in the skull of *Ornithorhynchus* there can be as little doubt that the anterior process is also the homologue of the mammalian vomer. The vomer in a half-grown Platypus, which has never been hitherto described, is particularly interesting. It does not extend so far forward as in most mammals; it appears in the middle of the palate between the maxillæ and the palatines; and it is at an early stage completely anchylosed with the basisphenoid. If the Dicynodont basisphenoid with the anchylosed "parasphenoid" were isolated and compared with the isolated basisphenoid and its anchylosed vomer in *Ornithorhynchus*, the agreement would be seen to be so striking that it would be no longer possible to doubt that the reptilian "parasphenoid" becomes the mammalian vomer.

One difficulty in getting generally accepted the view that the reptilian "parasphenoid" is the homologue of the mammalian vomer has been the condition in the Cynodonts. In the Cynodonts there is a very mammal-like secondary palate, and above the palate in the middle line is a somewhat mammal-like vomerine bone. But this bone is undoubtedly homologous with the anterior median bone which we have determined to be the prevomer in the Gorgonopsians. The pair of bones which are seen in the anterior palatal opening in the Cynodonts, and which thirty years ago I regarded as the prevomers, are now known to be the palatine processes of the premaxillæ.

If a Cynodont reptile were the mammalian ancestor there would be some difficulty in explaining the conversion of a long prevomer, which supports the secondary palate, into a short dumb-bell bone and its place being taken by a "parasphenoid" which lies far back in the skull; but notwithstanding the many mammal-like characters in the Cynodonts there have long been good reasons for believing that the mammals are not descended from a Cynodont. Years ago I suggested a Bauriamorph as the possible ancestor. Later I thought the ancestor may have been a primitive Gorgonopsian or Pre-gorgonopsian. WATSON has suggested a Therocephalian ancestry. But we have never hitherto been able to say with any certainty which family, or even Sub-order, gave rise to the mammalian stem. Now, however, I think we can say something definite.

In March of this year (1929) I found among the treasures of the Bloemfontein Museum two specimens of a remarkable new type of mammal-like reptile, which has not hitherto been described, but which Dr. VAN HOEPEN will have described before this paper appears. The specimens come from Ladybrand, O.F.S., and from the Cave Sandstone beds, which our leading authority on this matter (Dr. A. L. du Toit) regards as being of Rhætic Age. One specimen consists of the casts of most of the bones of the skull; the other of much of the skeleton and part of the skull badly weathered. The animal is a little mammal-like reptile, about the size of a small rat, but with a relatively large head. It took me some time to determine whether it is a mammal or a reptile. The lower jaw is very large and almost entirely formed by the dentary, but the hinge is between a small articular supported by small surangular, angular, and prearticular bones, and a small quadrate which rests on the squamosal. And though the dentary almost touches the squamosal it does not articulate with it, and we must thus place the animal among the reptiles, though it is almost a mammal.

Though the lower jaw resembles considerably that of a Cynodont, such as *Gomphognathus*, the palate differs very greatly and there can be no hesitation in making this little animal the type of a new Sub-order, and very little hesitation in stating that from a member of this Sub-order the mammals have been derived. In fact this new type is much nearer to the mammals than it is to any previously known Therapsid. In the present paper I shall only speak of the palate.

Though the palate is imperfect it can be restored with considerable confidence. In neither specimen is the front of the snout preserved, and the back part of the base of the skull, though present in both specimens, cannot be safely displayed. The middle portion of the palate is, however, well seen. There is certainly a large median vomer situated fairly well forward and completely dividing the pterygoids from each other, as in mammals. The anterior end of the vomer is lost, but most probably gave some support to the secondary palate. The pterygoids, so far as preserved, are almost typically mammalian. The prevomers probably formed a "dumb-bell" bone, which being loose has become lost, leaving the anterior palatal foramen as a large open space.

The discovery of this new link completely connects up the mammals with the Therapsids, but leaves us still in doubt as to the ancestry of this new Sub-order, which may be called the Ictidosauria. A number of previously imperfectly known forms probably belong to the same Sub-order. *Karoomys*, described by me 25 years ago from a single dentary bone, and which I regarded as a mammal, is evidently an Ictidosaurian from the upper Triassic beds. It is a small form, probably smaller than a mouse, and indeed the smallest known Therapsid. *Pachygenelus*, of Watson, also from Rhætic beds, is known only from an imperfect dentary, but fortunately with some well preserved teeth. Most probably it will also prove to be an Ictidosaurian. Then *Trithelodon*, a contemporary of *Pachygenelus*, known by little more than two maxillaries, is likely to prove a fourth genus of the Ictidosauria.

Possibly the Ictidosauria are derived from a Pre-Cynodont of Lower Triassic beds. Most of the known fossils from these beds are aquatic or semi-aquatic, and very little is known of the land forms. When a locality is discovered that yields a good variety of land animals I anticipate that we shall get the ancestors of the Ictidosauria and thus the remoter ancestors of the mammals.

It is unfortunate that we do not know the foot structure of the Ictidosauria, but most likely it will show the same digital formula as in mammals, 2, 3, 3, 3, 3, and thus agree with the Therocephalians, Bauriamorphs, Anomodonts, and Dromasaurians. In the Gorgonopsians, as I have shown, the formula is 2, 3, 4, 5, 3, with one phalanx in the third toe much reduced, and two reduced phalanges in the fourth. In Cynodonts, as seen in *Thrinaxodon*, the formula is still 2, 3, 4, 5, 3, but the reduced phalanges are quite rudimentary.

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DESCRIPTION OF PLATES.

Abbreviations.

A.At., Arch of Atlas; *Ang.*, Angular; *Art.*, Articular; *A.S.*, Alisphenoid; *B.O.* Basioccipital; *Cl.*, Clavicle; *Clm.*, Cleithrum; *Co.*, Coracoid; *Cor.*, Coronoid; *D.*, Dentary; *E.O.*, Exoccipital; *E.Pt.*, Epipterygoid; *Fr.*, Frontal; *H.*, Humerus; *I.Cl.*, Interclavicle; *I.P.*, Interparietal; *Ju.*, Jugal; *L.*, Lacrymal; *Mx.*, Maxilla; *Na.*, Nasal; *O.O.*, Opisthotic; *Pa.*, Parietal; *Pal.*, Palatine; *P.Art.*, Prearticular; *P.At.*, Proatlas; *P.Co.*, Precoracoid; *Pmx.*, Premaxilla; *P.O.*, Prootic; *Po.F.*, Postfrontal; *Po.O.*, Postorbital; *P.P.*, Preparietal; *P.Pmx.*, Palatine process of Premaxilla; *Pr.F.*, Prefrontal; *P.S.*, Presphenoid; *Pt.*, Pterygoid; *P.Vo.*, Prevomer; *Q.*, Quadrate; *Q.J.*, Quadratojugal; *R.*, Rib; *S.Ang.*, Surangular; *Sc.*, Scapula; *Smx.*, Septomaxilla; *S.O.*, Supraoccipital; *Sp.*, Splenial; *Sq.*, Squamosal; *St.*, Stapes; *Tb.*, Tabular; *T.P.*, Transpalatine or Ectopterygoid; *Vo.*, Vomer.

PLATE 27.

FIG. 1.—Skeleton of *Lycaenops ornatus*, BROOM, exactly as found. A little less than one-third natural size. A few other bones were found in the talus, of which the most important were the atlas, one cervical vertebra and two caudal vertebræ.

FIG. 2.—The right side of the skull of *Lycaenops ornatus*, BROOM, as preserved. The squamosal region is crushed much forward. About one-quarter natural size.

FIG. 3.—The remains of the shoulder girdle and right humerus with sternum, as found, of *Lycaenops ornatus*, BROOM. About one-quarter natural size.

FIG. 4.—The pelvic region with right hind limb of *Lycaenops ornatus*, BROOM, as preserved. About one-quarter natural size.

PLATE 28.

FIG. 5.—Occiput of *Lycaenops ornatus*, BROOM, about half natural size.

FIG. 6.—The epipterygoid, parts of pterygoid, vomer and basisphenoid of probably *Lycaenodon longiceps*, BROOM. Natural size.

FIG. 7.—Median section of the front portion of the skull of *Lycaenodon longiceps*, BROOM. Natural size.

FIG. 8.—Underside of left half of arch of atlas of *Lycaenops ornatus*, BROOM. About natural size.

FIG. 9.—The lower portion of the atlas of *Lycaenops ornatus*, BROOM. About natural size.

FIG. 10.—Upper view of proatlas and atlas of *Ælurognathus tigriceps* (BR. and HTN.). About half natural size.

FIG. 11.—Side view of axis vertebra of *Ælurognathus tigriceps* (BR. and HTN.). About half natural size.

FIG. 12.—Upper view of 3rd, 4th, 5th, 6th and 7th cervical vertebræ of *Ælurognathus tigriceps* (BR. and HTN.). About half natural size.

FIG. 13.—Side view of 5th cervical vertebra of *Ælurognathus tigriceps* (BR. and HTN.). About half natural size.

FIG. 14.—Outer view of lower half of left shoulder girdle of *Lycaenops ornatus*, BROOM. About two-thirds natural size.

FIG. 15.—Inner view of lower part of left shoulder girdle with top of humerus of *Lycaenops ornatus*, BROOM. About two-thirds natural size.

FIG. 16.—Side view of right shoulder girdle of *Scylacops capensis*, BROOM, showing cleithrum in position. About half natural size.

FIG. 17.—Front view of sternum of *Lycaenops ornatus*, BROOM, somewhat crushed on left side. About two-thirds of natural size.

FIG. 18.—Outer view of right pelvic girdle of *Lycaenops ornatus*, BROOM. A little more than half natural size.

PLATE 29.

FIG. 19.—Restoration of the skull of *Galesuchus gracilis*, HTN. About three-quarters natural size.

FIG. 20.—Parietal region of *Lycaenoides angusticeps*, BROOM. About half natural size.

FIG. 21.—Skull of *Scylacognathus parvus*, BROOM. About three-quarters natural size.

FIG. 22.—Restoration of skull of *Cynarioides tenuis*, BROOM. About three-quarters natural size.

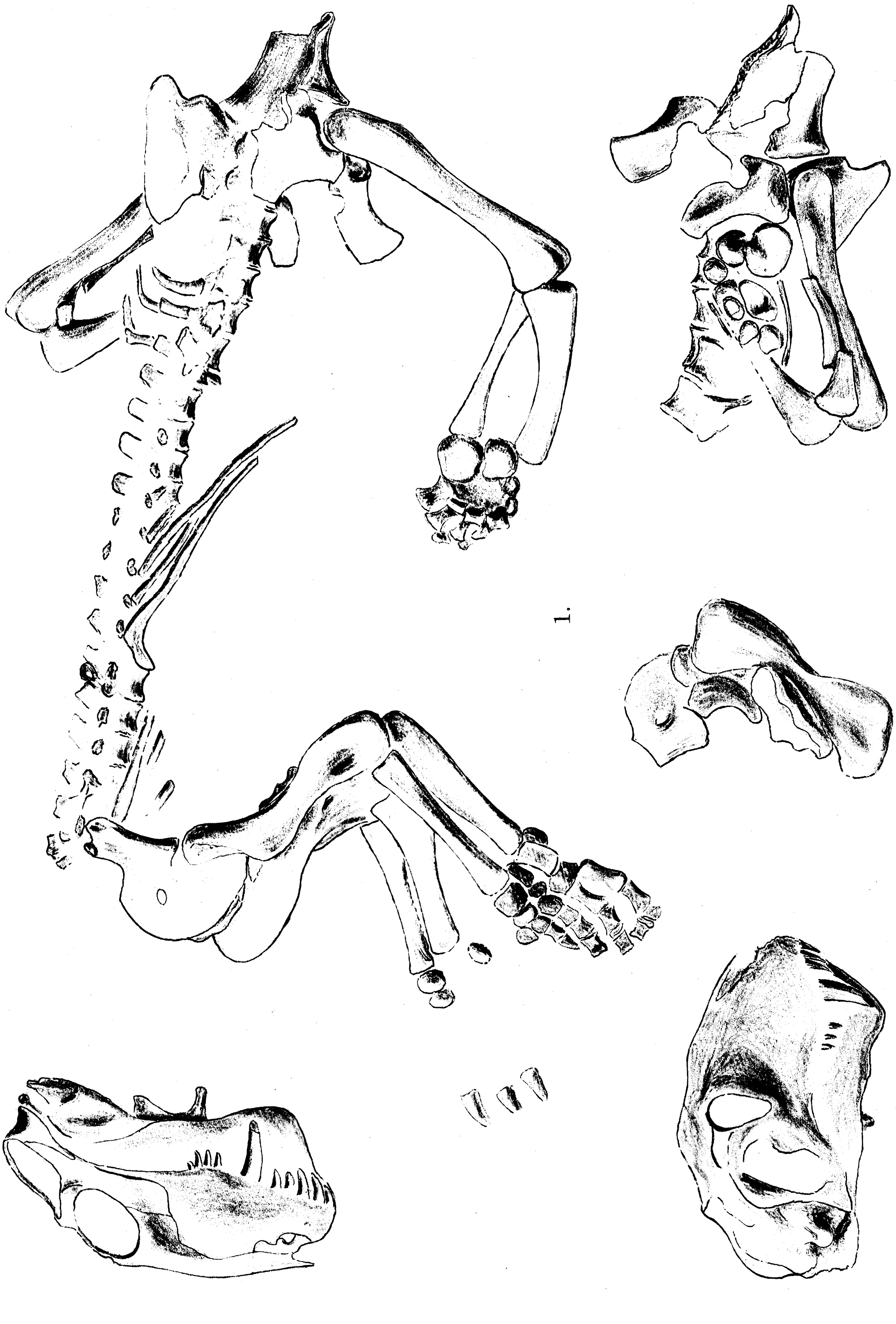
FIG. 23.—Skull of *Sycosaurus laticeps*, HAUGHTON. About two-fifths natural size.

FIG. 24.—Parietal and frontal regions of *Scylacops capensis*, BROOM. About three-fifths natural size.

FIG. 25.—Snout of *Lycaenodon longiceps*, BROOM. About half natural size.

FIG. 26.—Greater part of skull of *Cynariops robustus*, BROOM. About three-fifths natural size.

FIG. 27.—Skull of *Lycaenops ornatus*, BROOM. All the figures are reduced. About half natural size.



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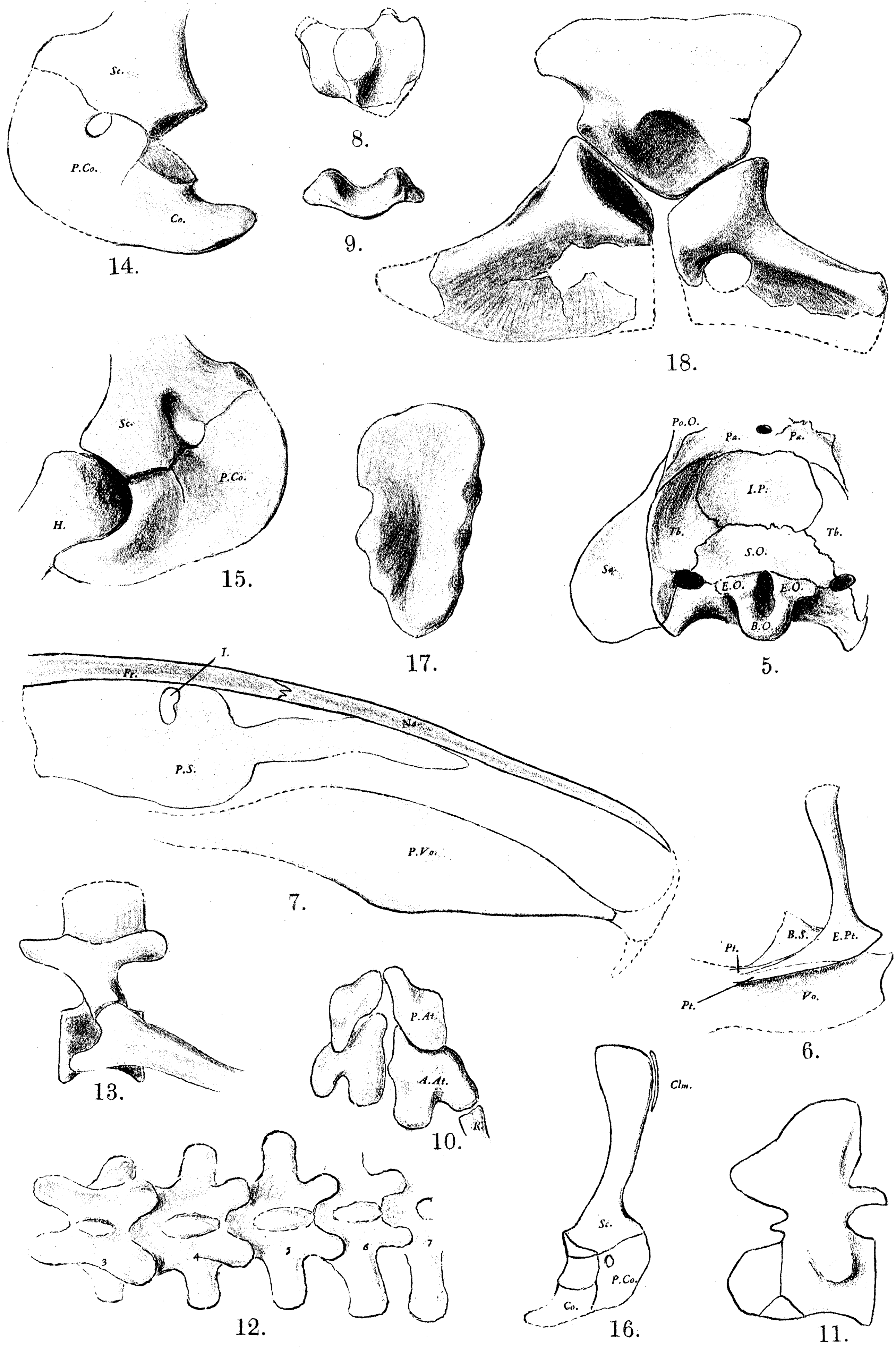
LYCÆNOPS ORNATUS, BROOM.

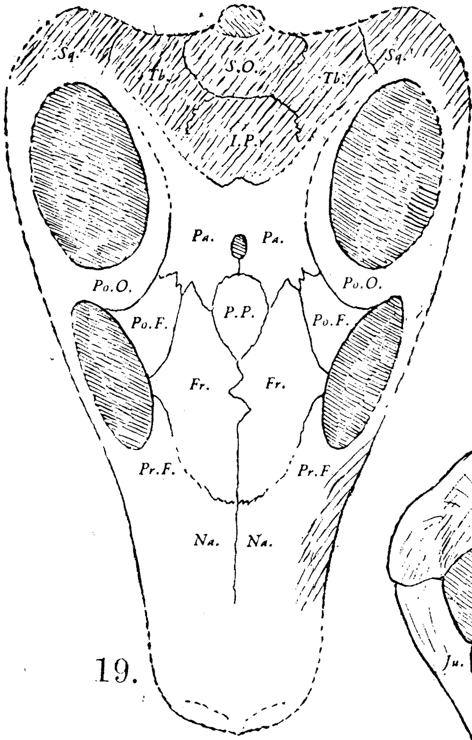
R. BROOM *del.*

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



R. BROOM *del.*

DETAILS OF SKELETON OF VARIOUS GORGONOPSIANS.



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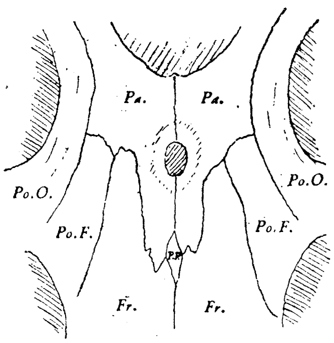

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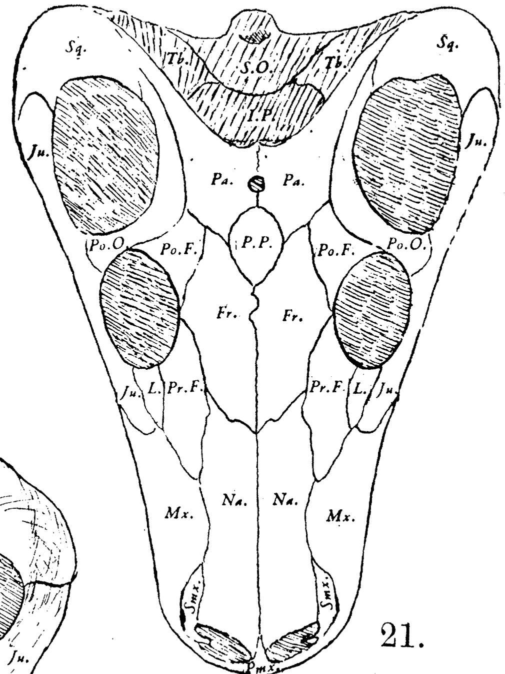

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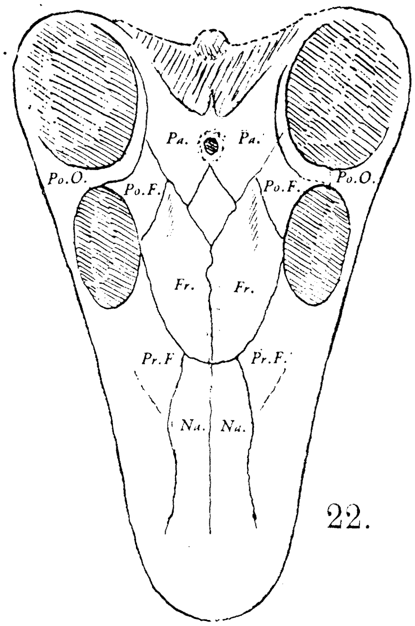

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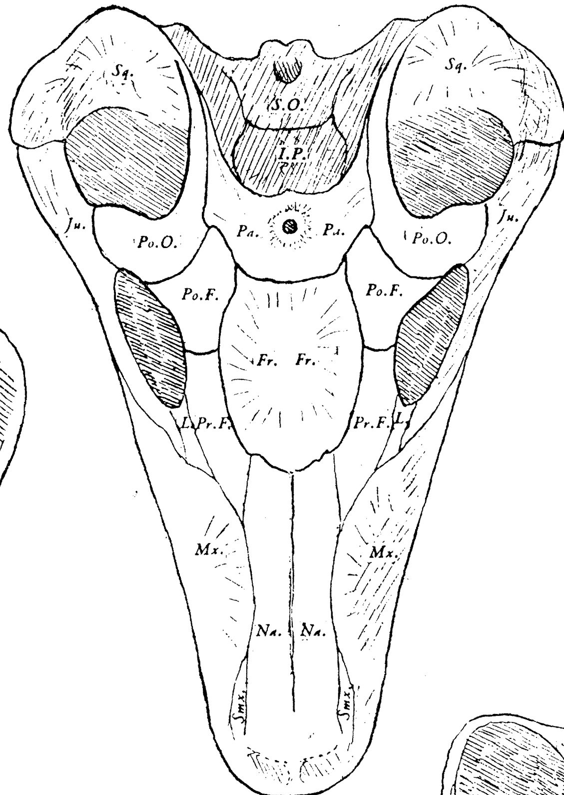

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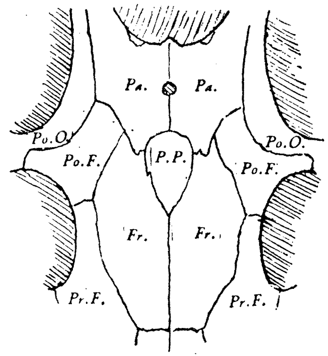

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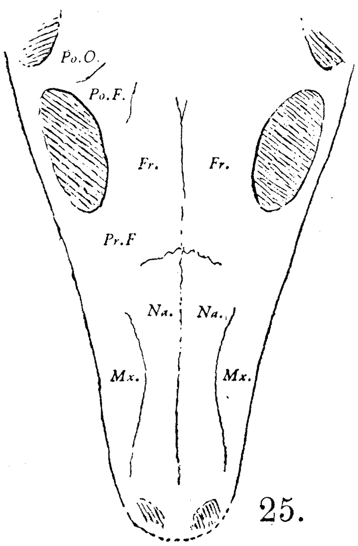

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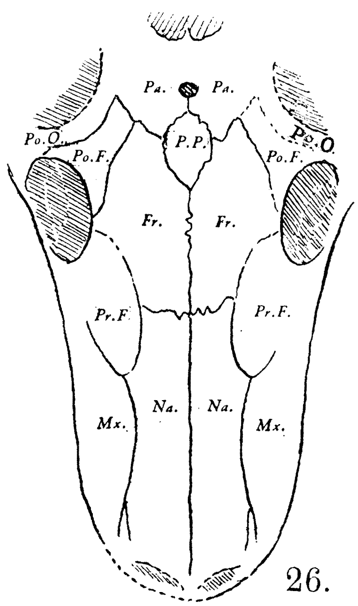

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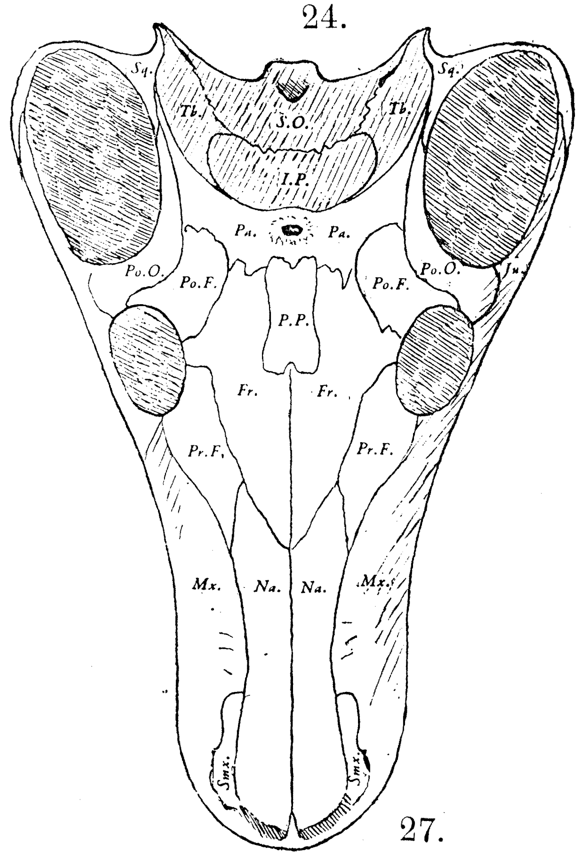

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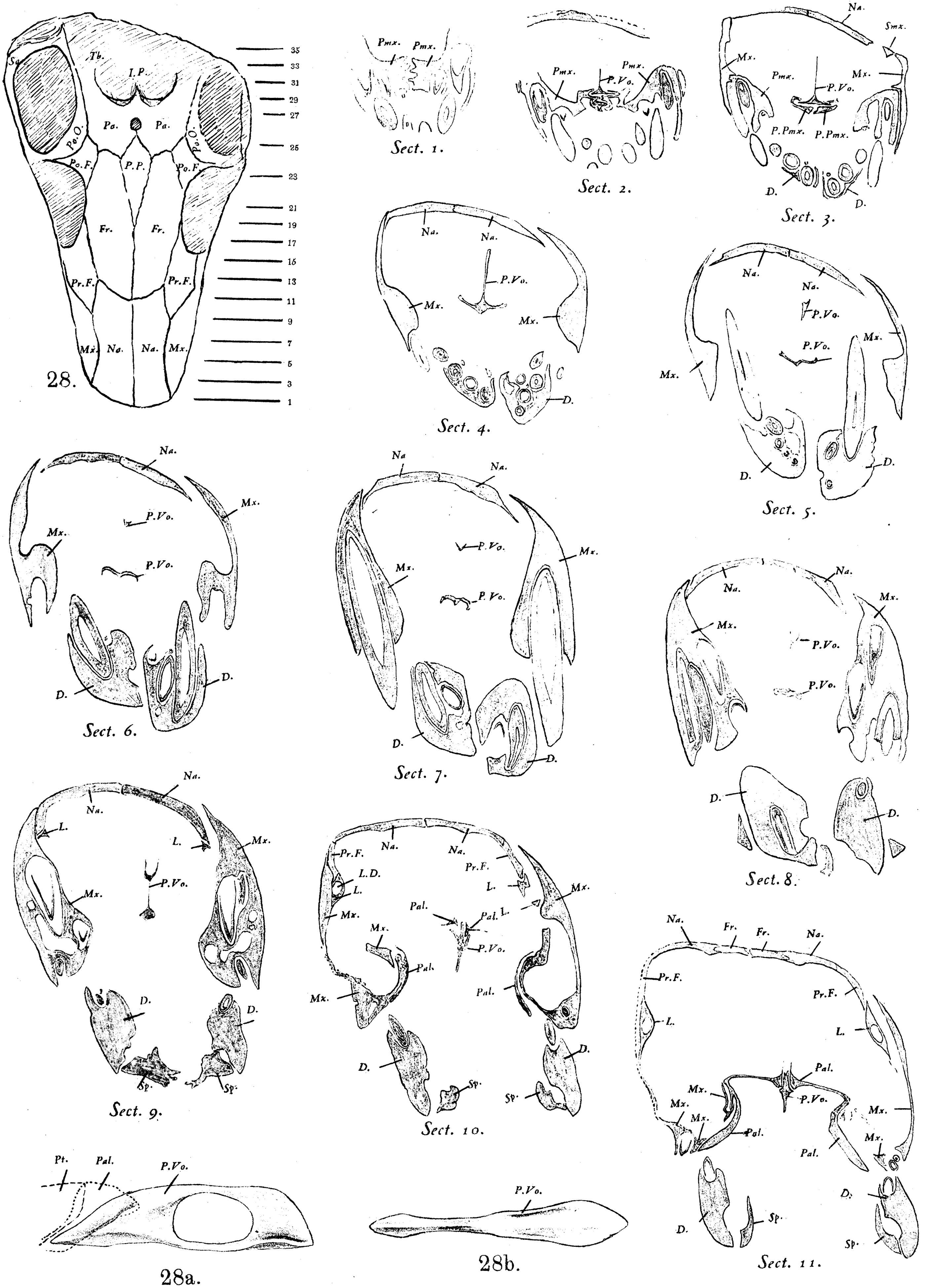
R. BROOM *del.*

SKULLS OF VARIOUS GORGONOPSIANS.



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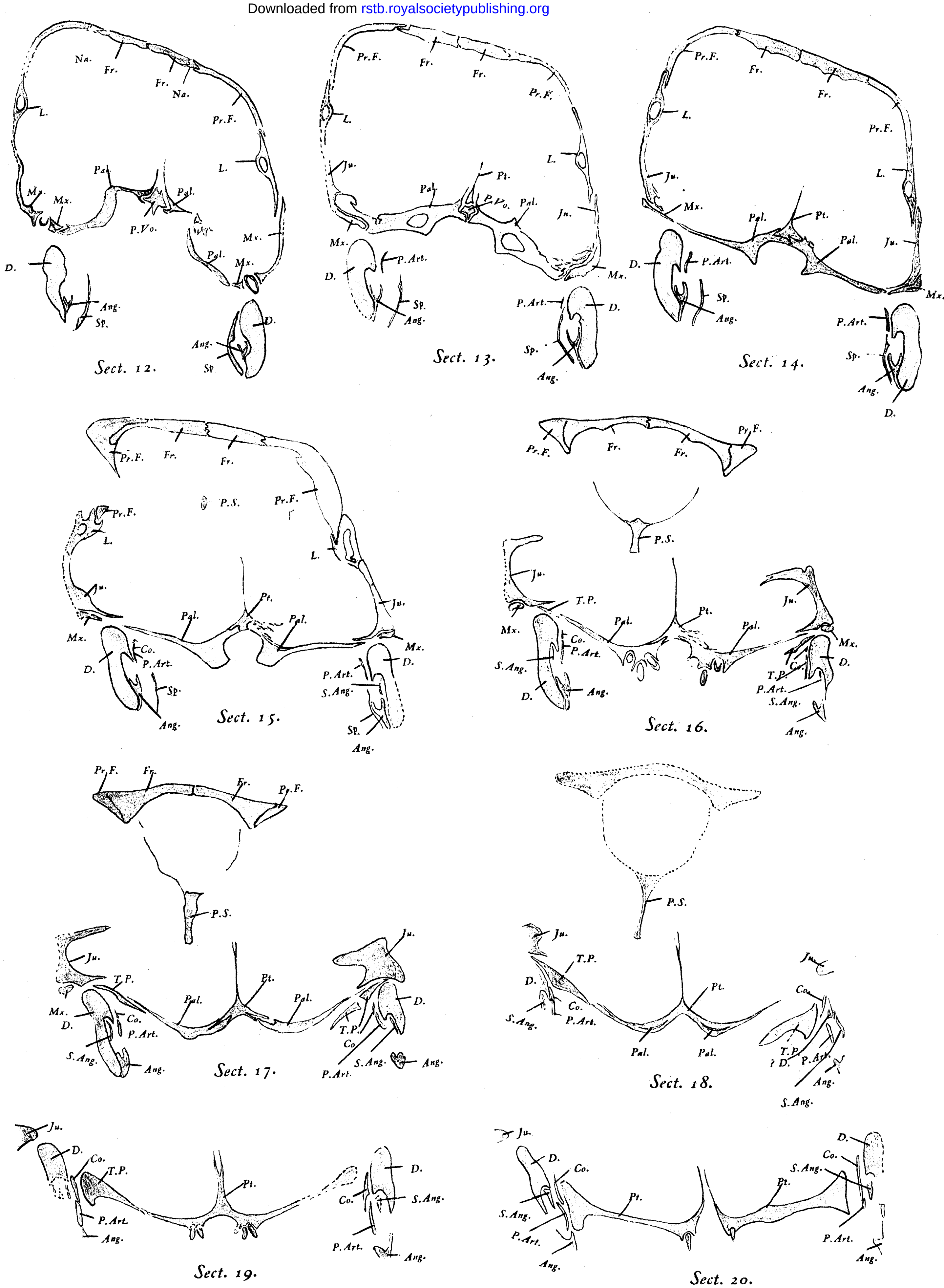
SKULL OF CYNARIOIDES GRACILIS, Broom.



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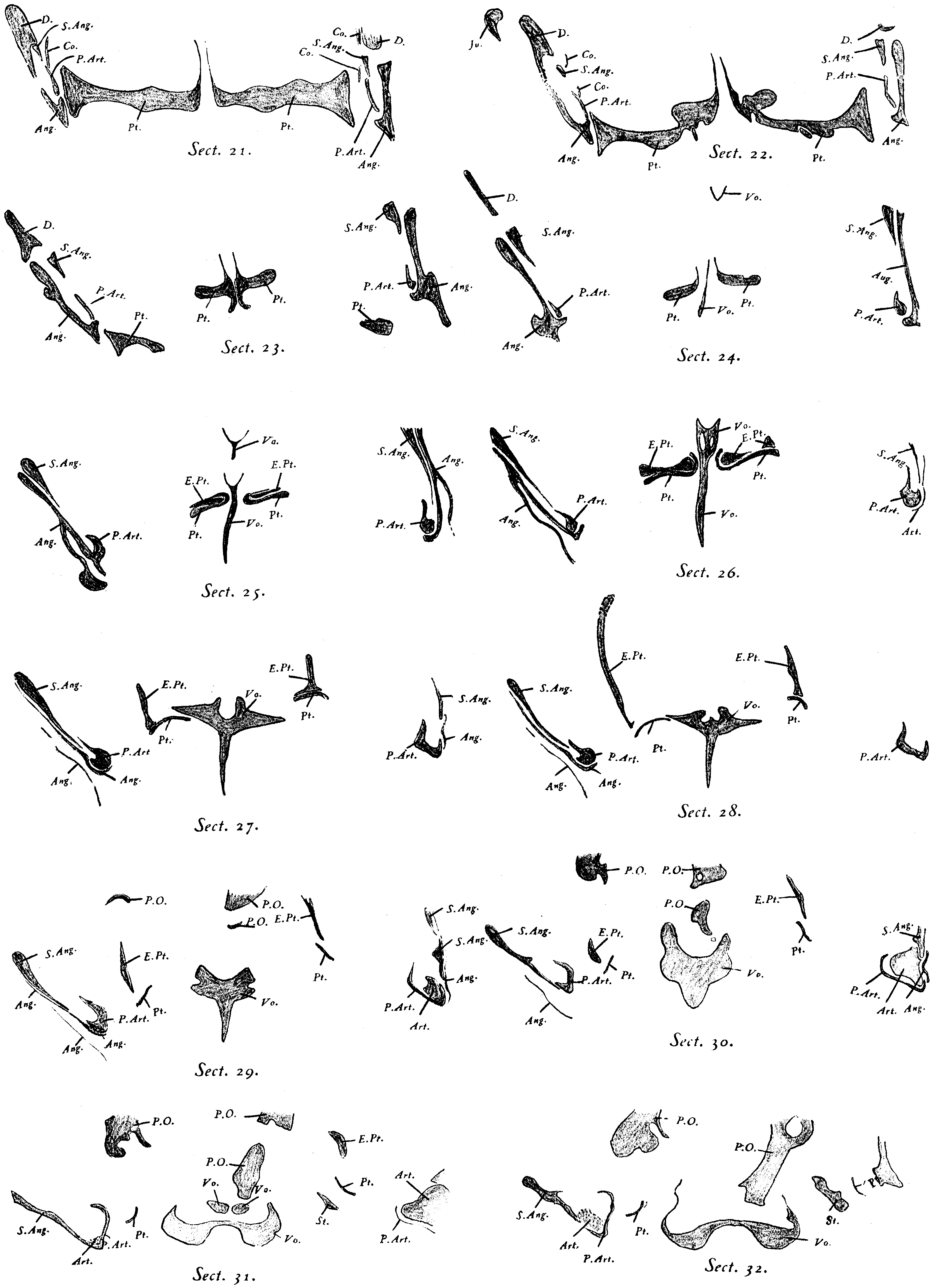

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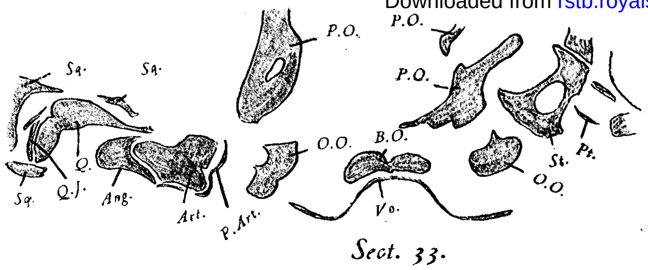

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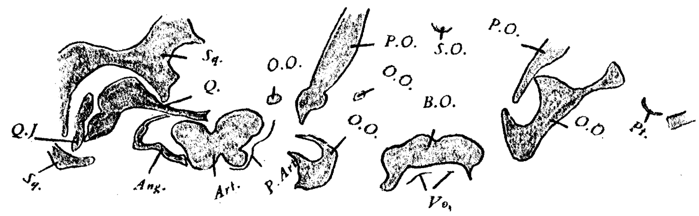

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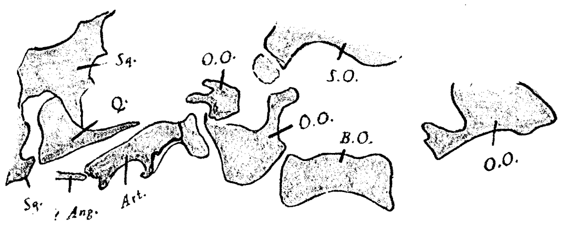

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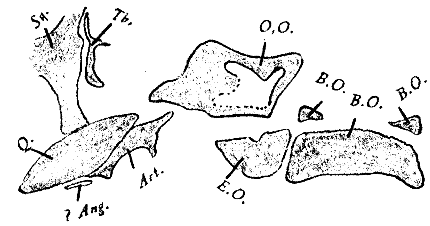

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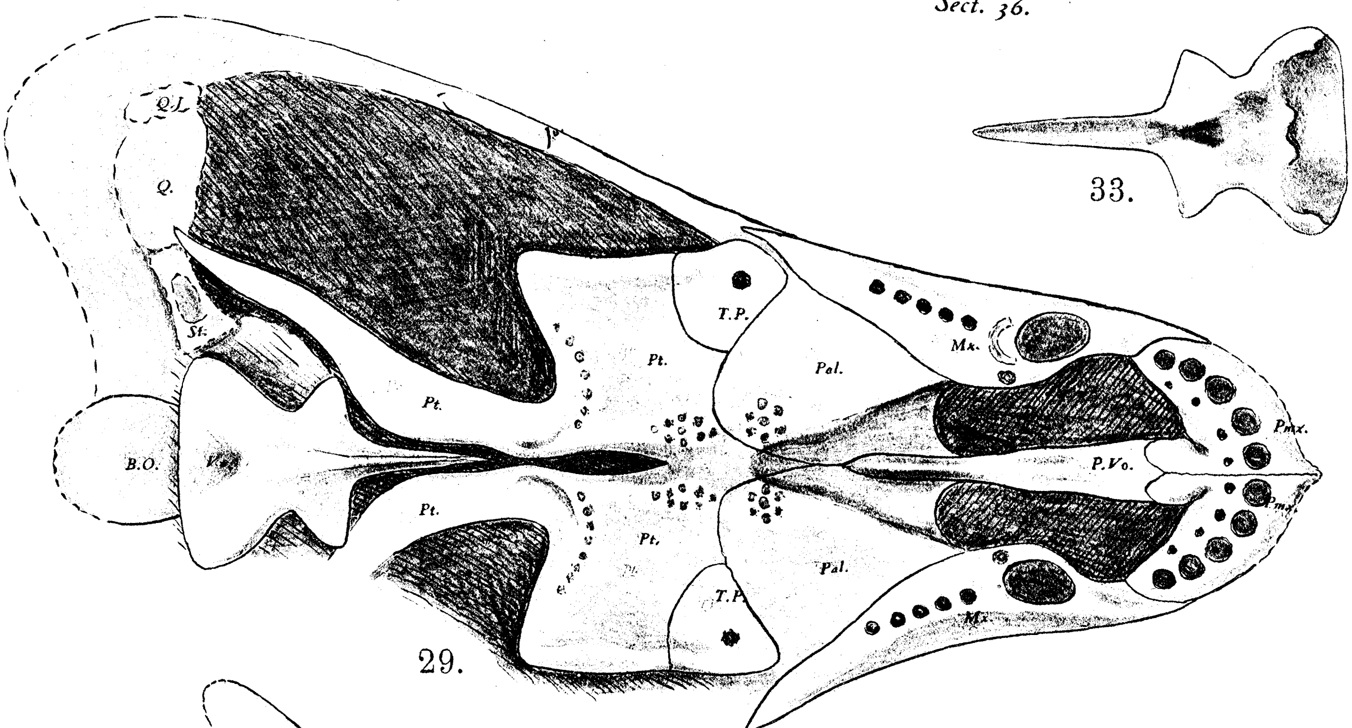

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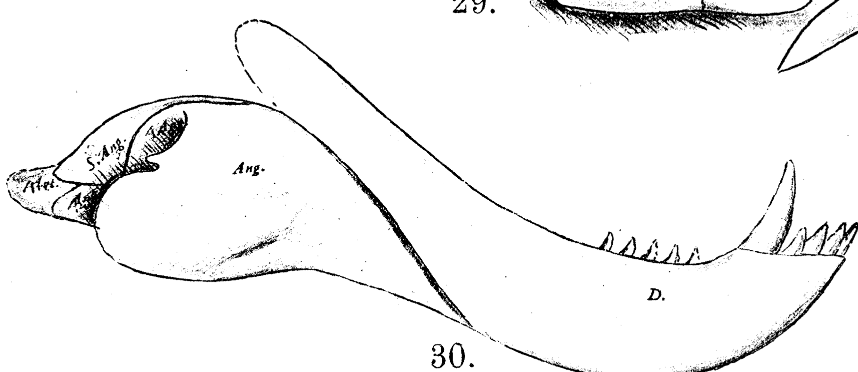

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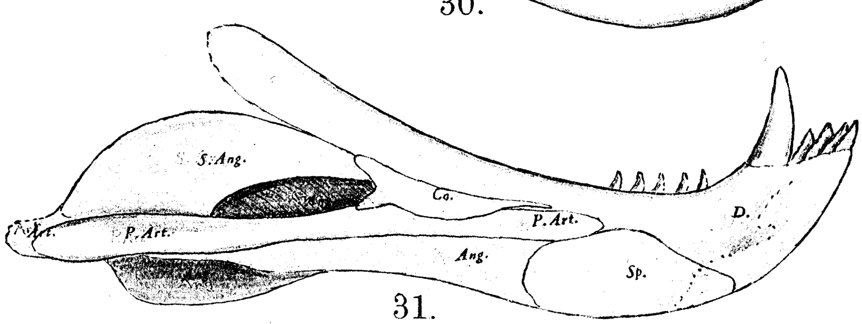

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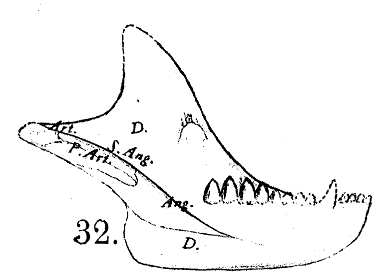

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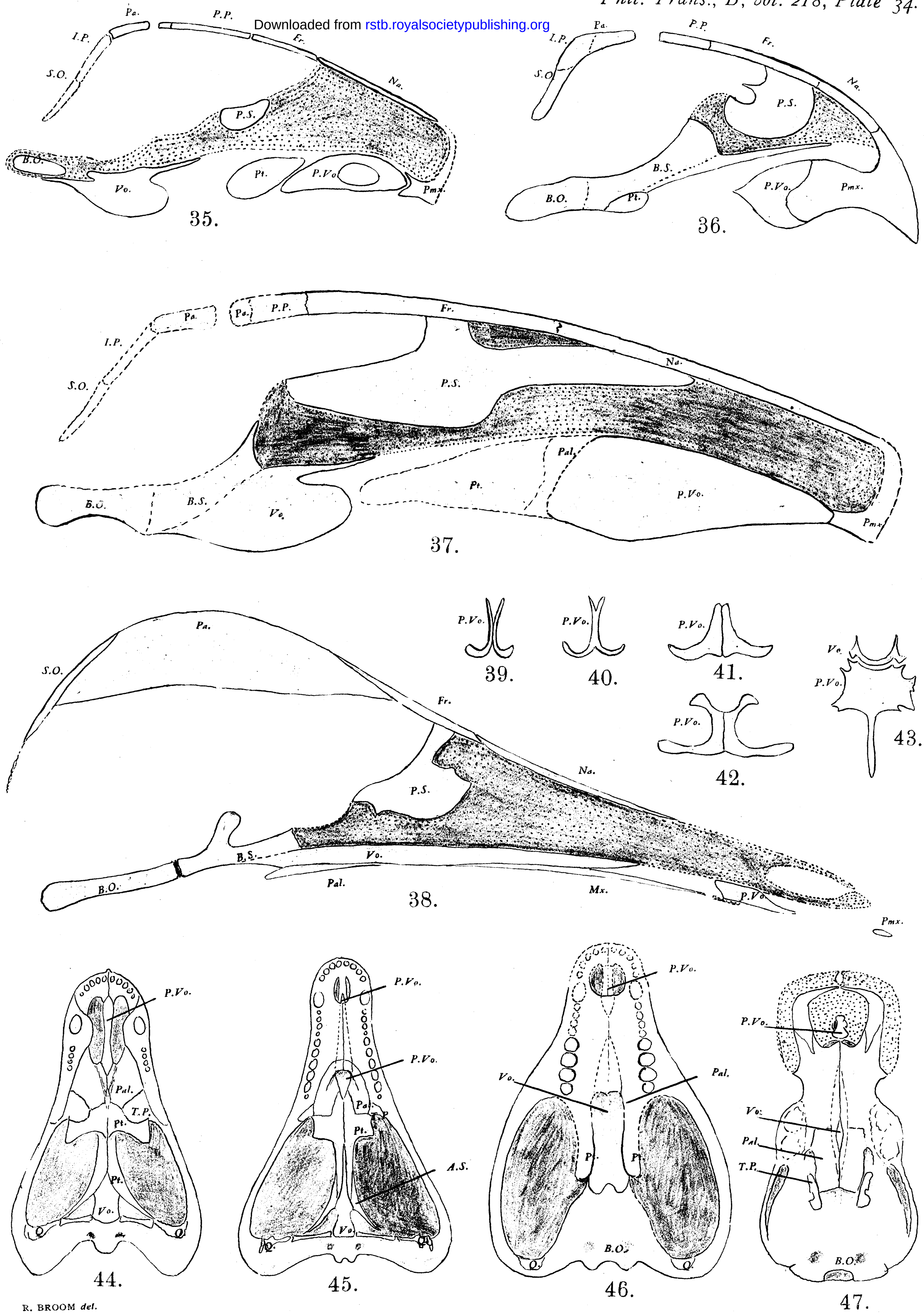
CYNARIOIDES GRACILIS, BROOM.



R. BROOM del.

RELATIONS OF VOMER AND PREVOMER IN REPTILES AND ORNITHORHYNCHUS.

PLATE 30.

FIG. 28.—Upper view of the skull of *Cynarioides gracilis*, BROOM. Natural size, with indications of the positions of each section figured. Sections 1 to 11 described in the paper—all twice natural size.

FIG. 28A.—Side view of prevomer of same. Restored from sections. Twice natural size.

FIG. 28B.—Under view of prevomer. Restored from sections. Twice natural size.

PLATE 31.

Sections 12 to 20.—Transverse sections of the skull of *Cynarioides gracilis*, BROOM. All twice natural size. Described in the paper.

PLATE 32.

Sections 21–32.—Skull of *Cynarioides gracilis*, BROOM. All twice natural size. Described in the paper.

PLATE 33.

Sections 33–36.—Skull of *Cynarioides gracilis*, BROOM. All twice natural size. Described in the paper.

FIG. 29.—Reconstruction of Palate of *C. gracilis*, BROOM. Twice natural size.

FIG. 30.—Reconstruction of outer side of Mandible of *C. gracilis*, BROOM. One and a-half times natural size.

FIG. 31.—Reconstruction of inner side of Mandible of *C. gracilis*, BROOM. One and a-half times natural size.

FIG. 32.—Inner side of Mandible of a Cave Sandstone Therapsid showing the great reduction of the bones other than the dentary. Natural size.

FIG. 33.—Upper side of vomer of *C. gracilis*, BROOM. Reconstructed from sections. Twice natural size.

FIG. 34.—Side view of vomer of *C. gracilis*, BROOM. Reconstructed from sections. Twice natural size.

PLATE 34.

FIG. 35.—Reconstructed median section of the skull of *Cynarioides gracilis*, BROOM. About six-fifths natural size.

FIG. 36.—Median section of skull of young *Dicynodon Sollasi*, BROOM. Natural size.

FIG. 37.—Median section of skull of *Lycœnodon longiceps*, BROOM. Natural size. Anterior two-thirds from type specimen. Posterior region restored from crushed specimen which I believe to belong to same species.

FIG. 38.—Median section of skull of young *Ornithorhynchus anatinus*, SHAW. Almost three times natural size.

FIG. 39.—Section across the prevomers of the small Therocephalian *Ictidognathus hemburyi*, BROOM. About three times natural size.

FIG. 40.—Section across the united prevomers of a small undescribed Therocephalian. Enlarged about five times.

FIG. 41.—Section across the prevomers of *Sphenodon punctatus*, GRAY. Enlarged about four times.

FIG. 42.—Section across the prevomers of *Ornithorhynchus anatinus*, SHAW. Enlarged about six times.

FIG. 43.—Section across the united prevomers and the vomer of *Dicynodon platyceps*, BROOM. Natural size.

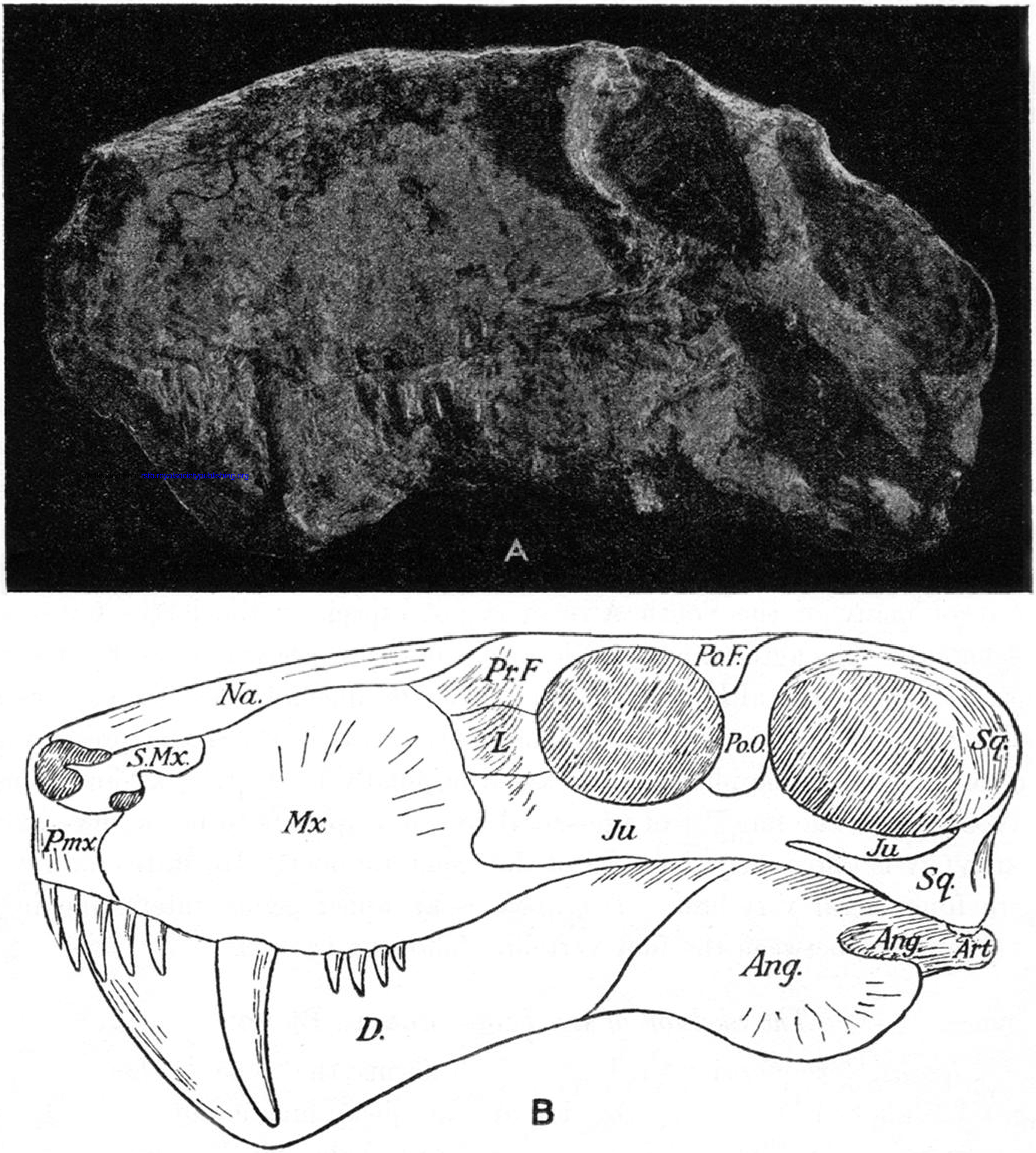
FIG. 44.—Base of skull (palate) of the Gorgonopsian *Scylacops capensis*, BROOM. Reduced.

FIG. 45.—Base of skull of the Cynodont *Cynidiognathus longiceps*, HAUGHTON. Reduced.

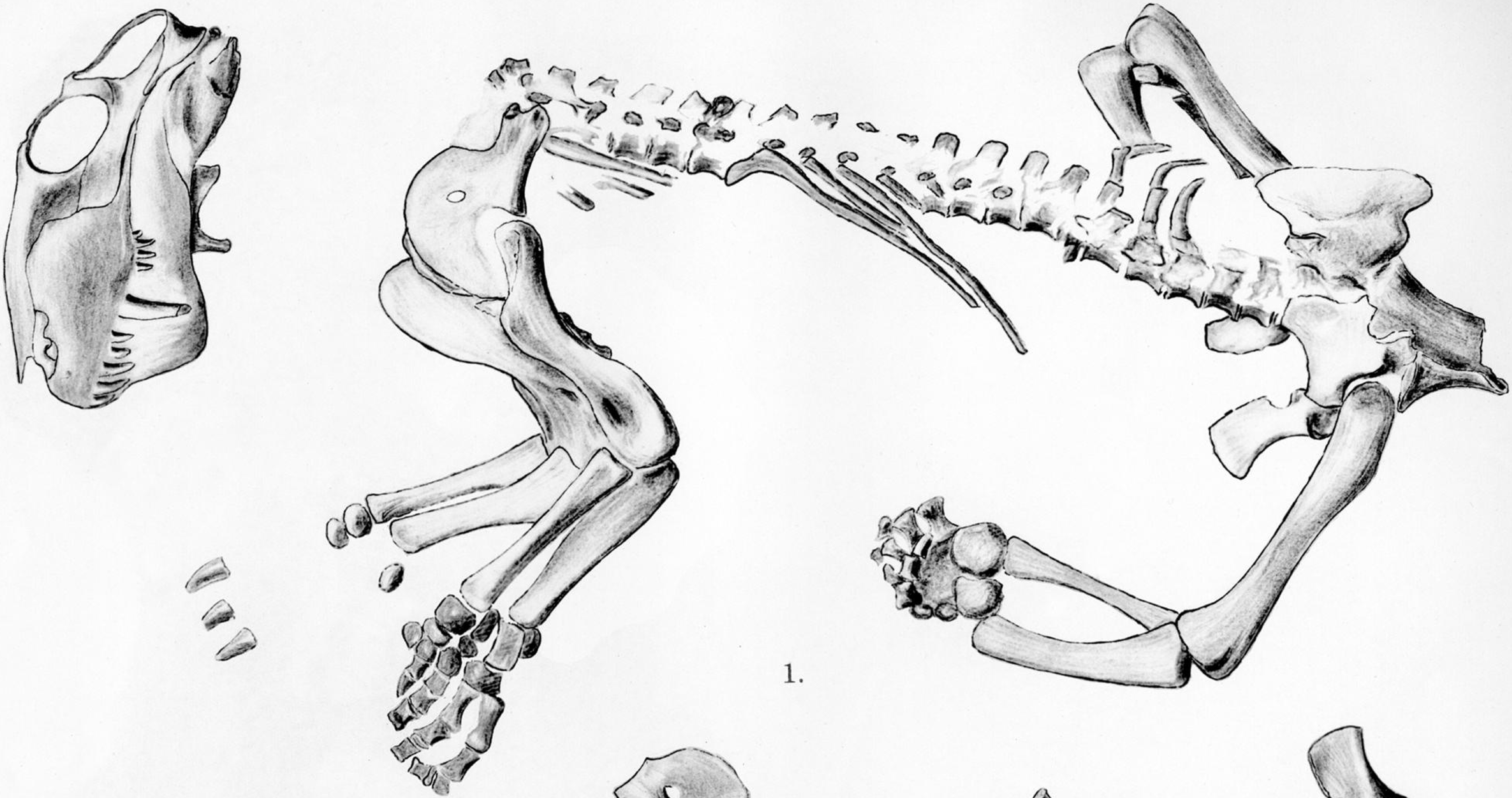
FIG. 46.—Base of skull of undescribed higher Therapsid, Ictidosaurian. Reduced.

FIG. 47.—Base of skull of young *Ornithorhynchus anatinus*, SHAW. Natural size.

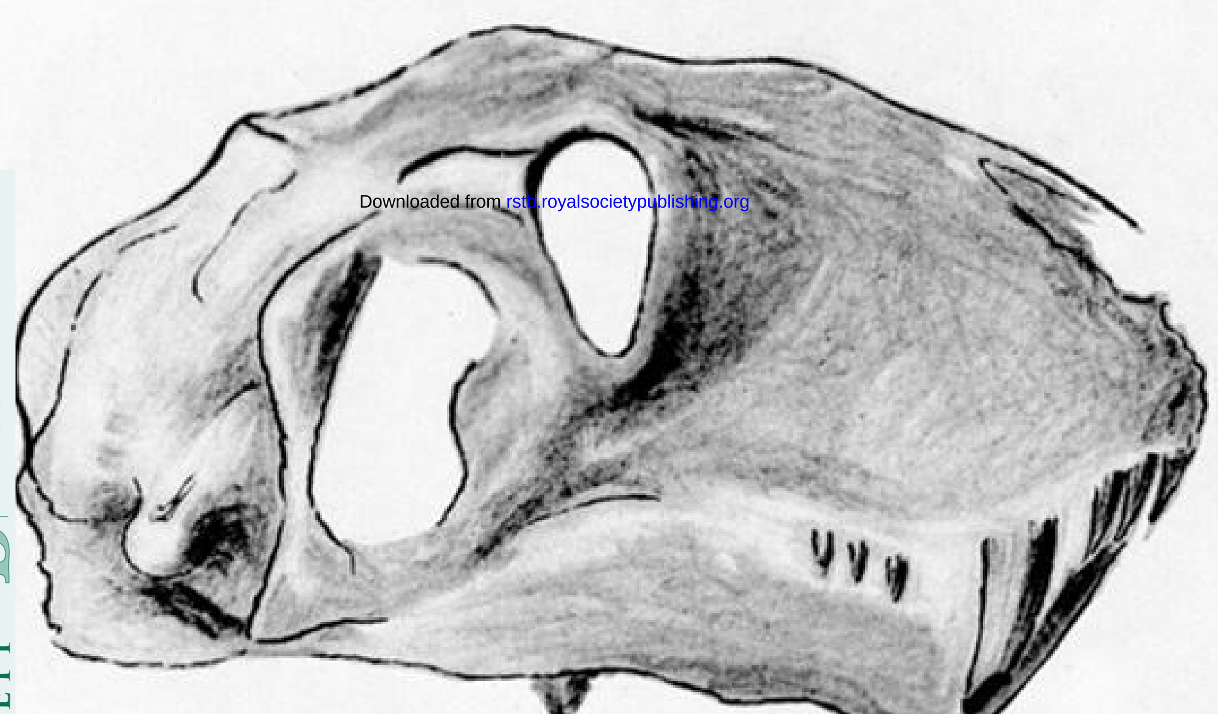
(These four views show evolution of prevomers and vomer through the Therapside to the Mammal.)



Text-fig. 1.—Skull of *Lycænops ornatus*, Broom. About ½ nat. size. A, as preserved; B, outline with distortion corrected.



1.



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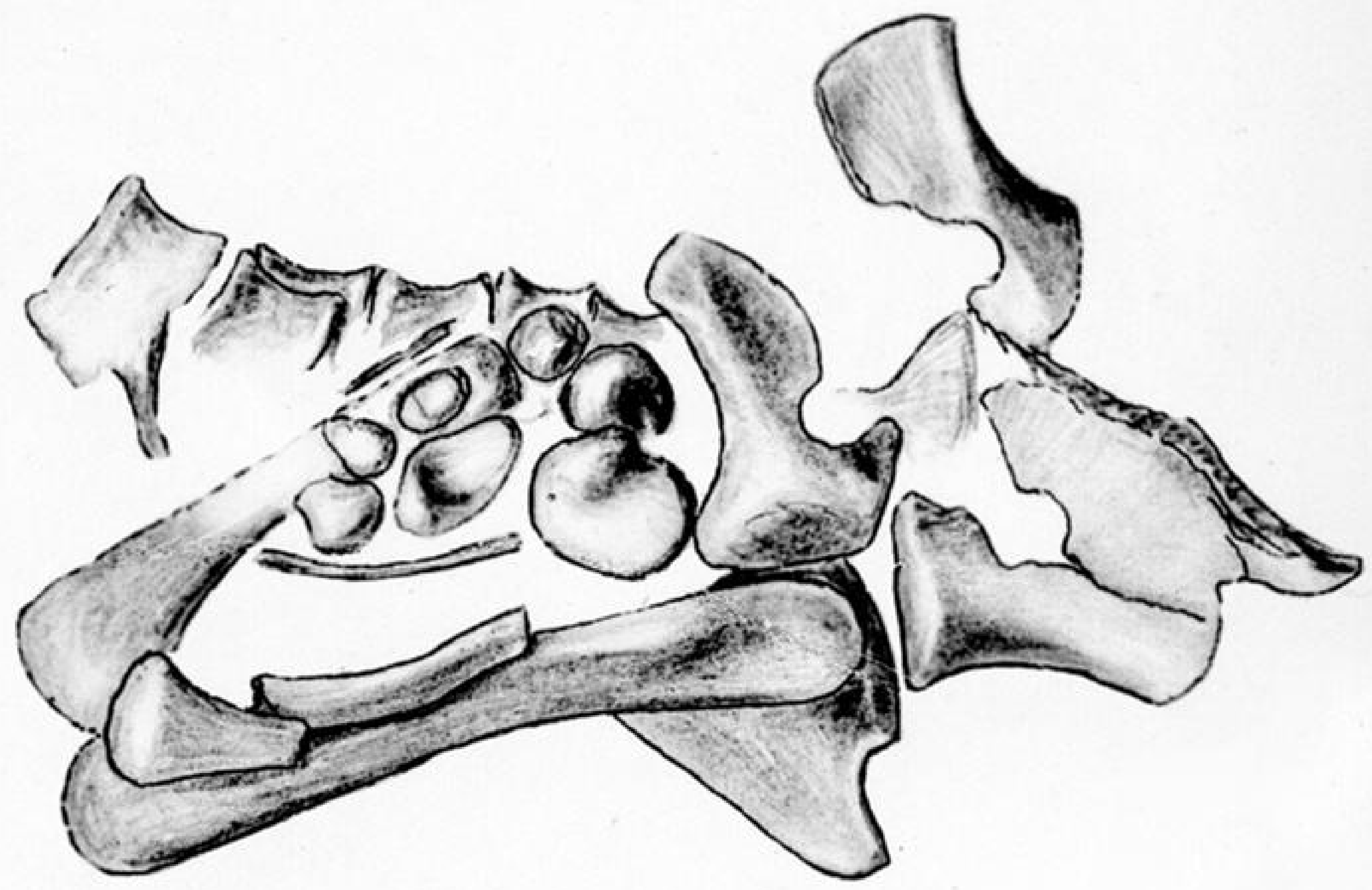


4.

LYCÆNOPS ORNATUS, BROOM.

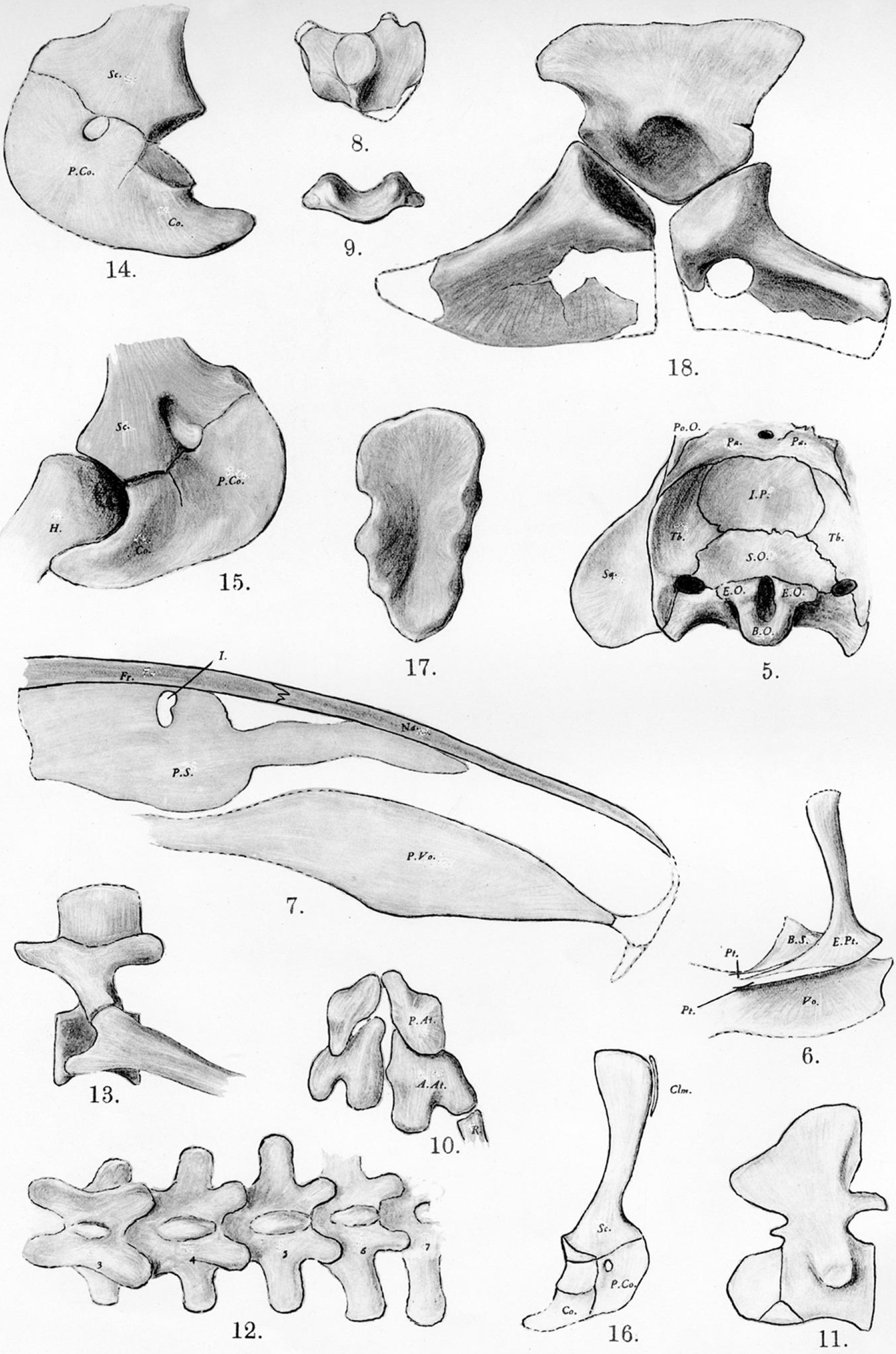
PLATE 27.

FIG. 1.—Skeleton of *Lycaenops ornatus*, BROOM, exactly as found. A little less than one-third natural size. A few other bones were found in the talus, of which the most important were the atlas, one cervical vertebra and two caudal vertebræ.

FIG. 2.—The right side of the skull of *Lycaenops ornatus*, BROOM, as preserved. The squamosal region is crushed much forward. About one-quarter natural size.

FIG. 3.—The remains of the shoulder girdle and right humerus with sternum, as found, of *Lycaenops ornatus*, BROOM. About one-quarter natural size.

FIG. 4.—The pelvic region with right hind limb of *Lycaenops ornatus*, BROOM, as preserved. About one-quarter natural size.



DETAILS OF SKELETON OF VARIOUS GORGONOPSIANS.

Plate 28.

Fig. 5.—Occiput of *Lycaenops ornatus*, Broom, about half natural size.

Fig. 6.—The epipterygoid, parts of pterygoid, vomer and basisphenoid of probably *Lycaenodon longiceps*, Broom. Natural size.

Fig. 7.—Median section of the front portion of the skull of *Lycaenodon longiceps*, Broom. Natural size.

Fig. 8.—Underside of left half of arch of atlas of *Lycaenops ornatus*, Broom. About natural size.

Fig. 9.—The lower portion of the atlas of *Lycaenops ornatus*, Broom. About natural size.

Fig. 10.—Upper view of proatlas and atlas of *Ælurognathus tigriceps* (Br. and Htn.). About half natural size.

Fig. 11.—Side view of axis vertebra of *Ælurognathus tigriceps* (Br. and Htn.). About half natural size.

Fig. 12.—Upper view of 3rd, 4th, 5th, 6th and 7th cervical vertebræ of *Ælurognathus tigriceps* (Br. and Htn.). About half natural size.

Fig. 13.—Side view of 5th cervical vertebra of *Ælurognathus tigriceps* (Br. and Htn.). About half natural size.

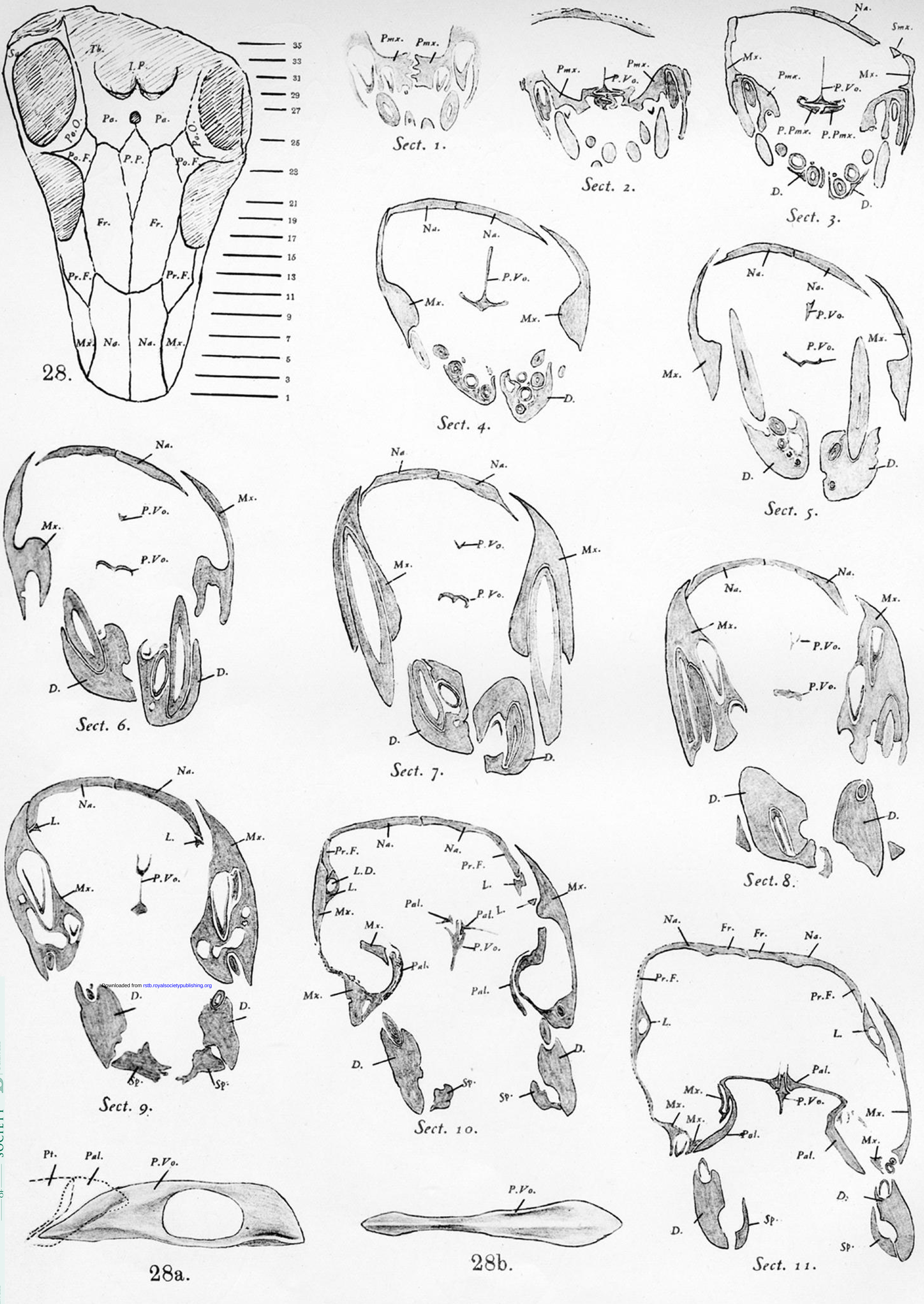
Fig. 14.—Outer view of lower half of left shoulder girdle of *Lycaenops ornatus*, Broom. About two-thirds natural size.

Fig. 15.—Inner view of lower part of left shoulder girdle with top of humerus of *Lycaenops ornatus*, Broom. About two-thirds natural size.

Fig. 16.—Side view of right shoulder girdle of *Scylacops capensis*, Broom, showing cleithrum in position. About half natural size.

Fig. 17.—Front view of sternum of *Lycaenops ornatus*, Broom, somewhat crushed on left side. About two-thirds of natural size.

Fig. 18.—Outer view of right pelvic girdle of *Lycaenops ornatus*, Broom. A little more than half natural size.



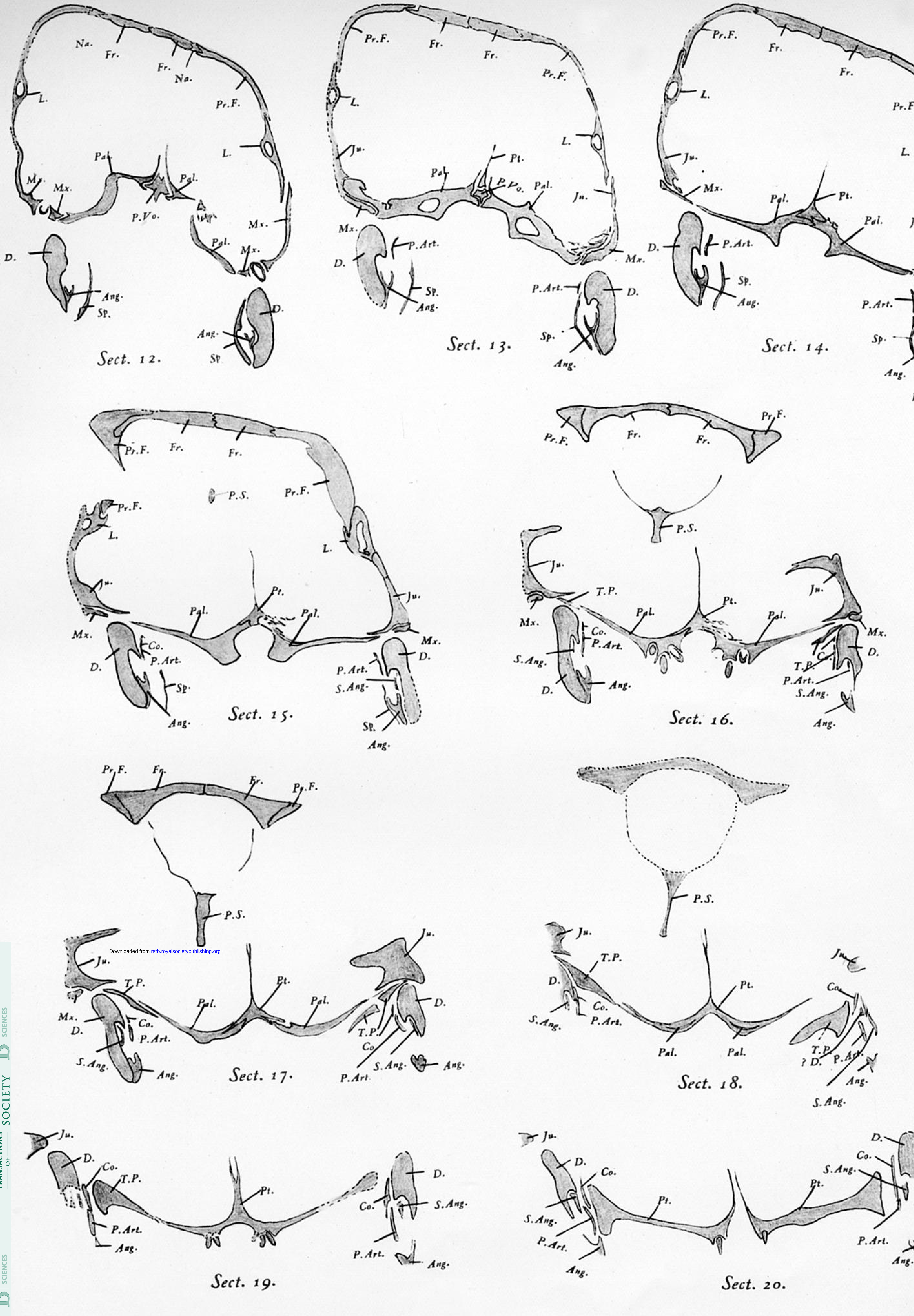
SKULL OF CYNARIOIDES GRACILIS, BROOM.

PLATE 30.

FIG. 28.—Upper view of the skull of *Cynarioides gracilis*, BROOM. Natural size, with indications of the positions of each section figured. Sections 1 to 11 described in the paper—all twice natural size.

FIG. 28A.—Side view of prevomer of same. Restored from sections. Twice natural size.

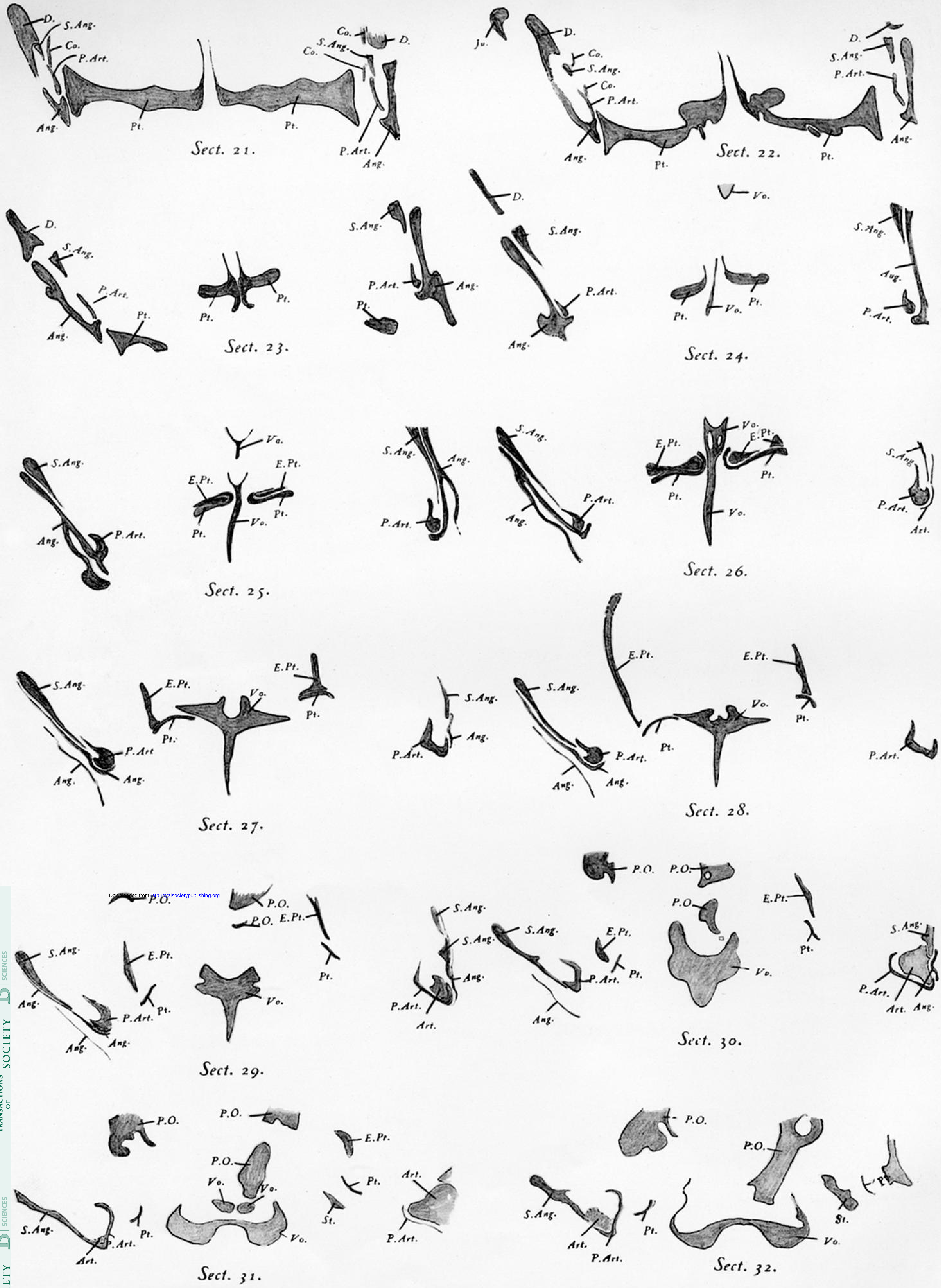
FIG. 28B.—Under view of prevomer. Restored from sections. Twice natural size.



SECTIONS OF SKULL OF CYNARIOIDES GRACILIS, Broom.

Plate 31.

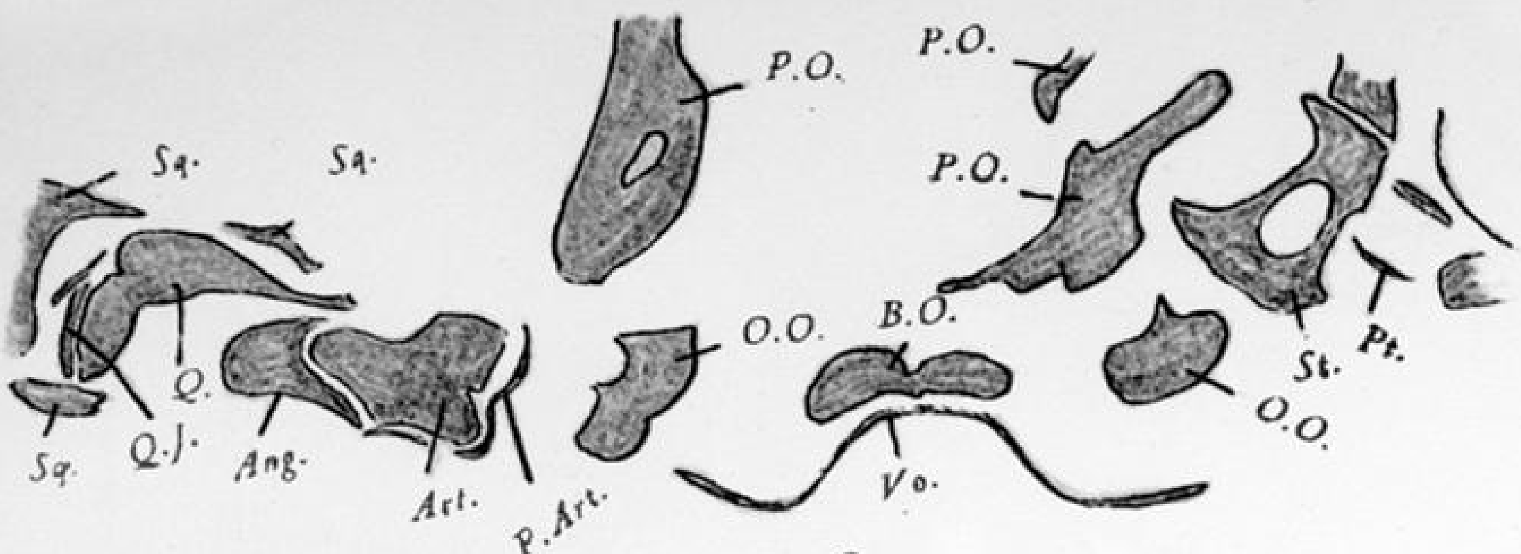
Sections 12 to 20.—Transverse sections of the skull of *Cynarioides gracilis*, Broom. All twice natural size. Described in the paper.



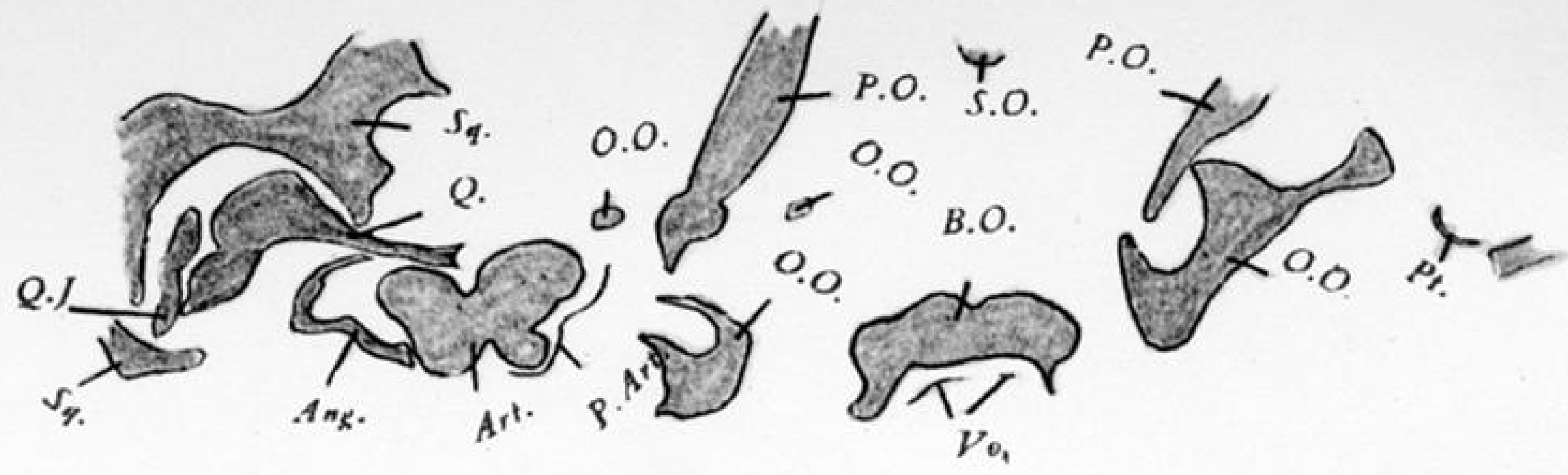
SECTIONS OF SKULL OF CYNARIOIDES GRACILIS, BROOM.

PLATE 32.

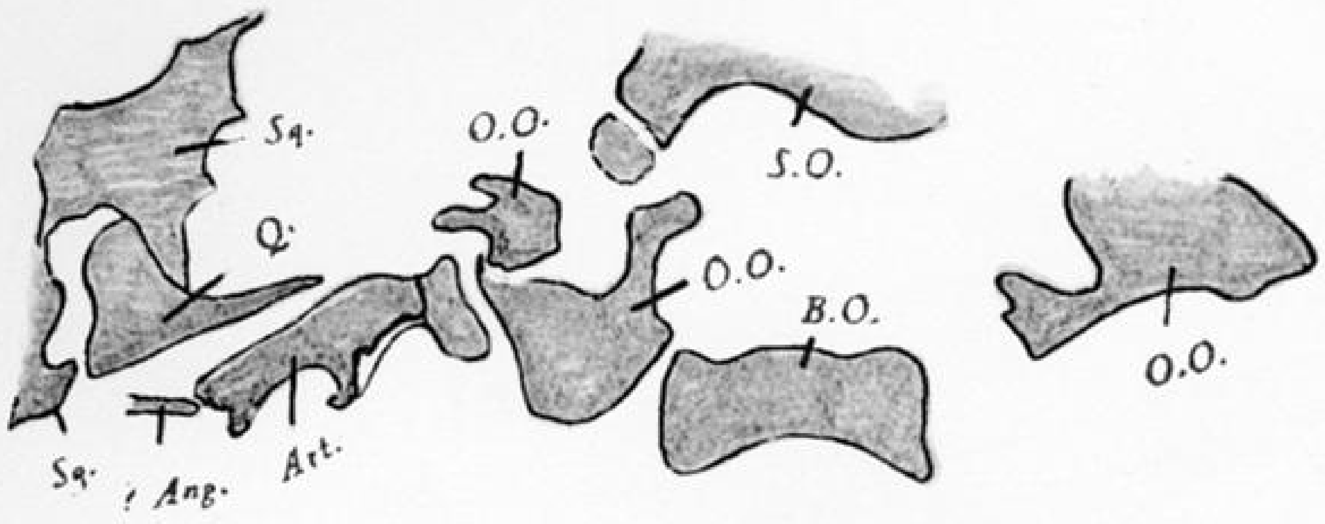
Sections 21–32.—Skull of *Cynarioides gracilis*, BROOM. All twice natural size. Described in the paper.



Sect. 33.



Sect. 34.



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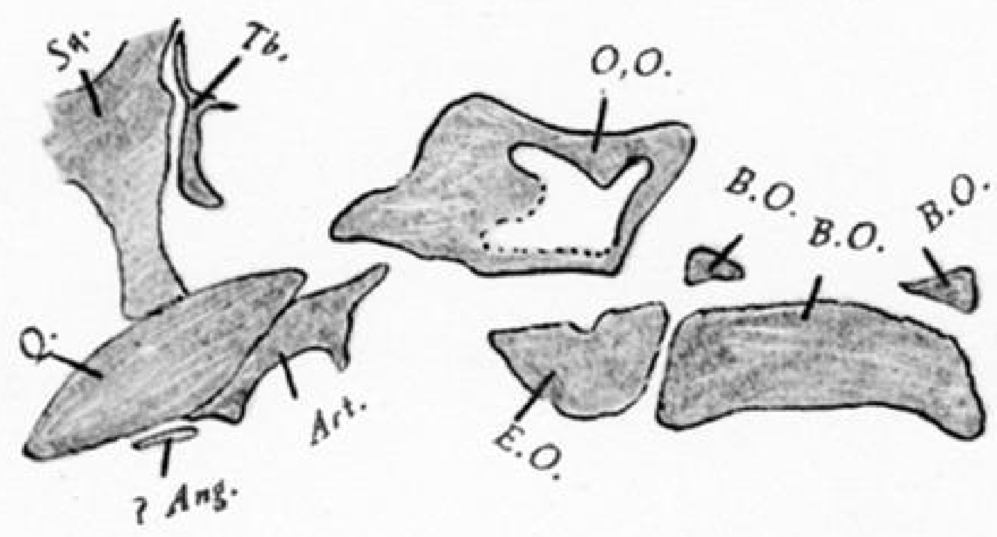
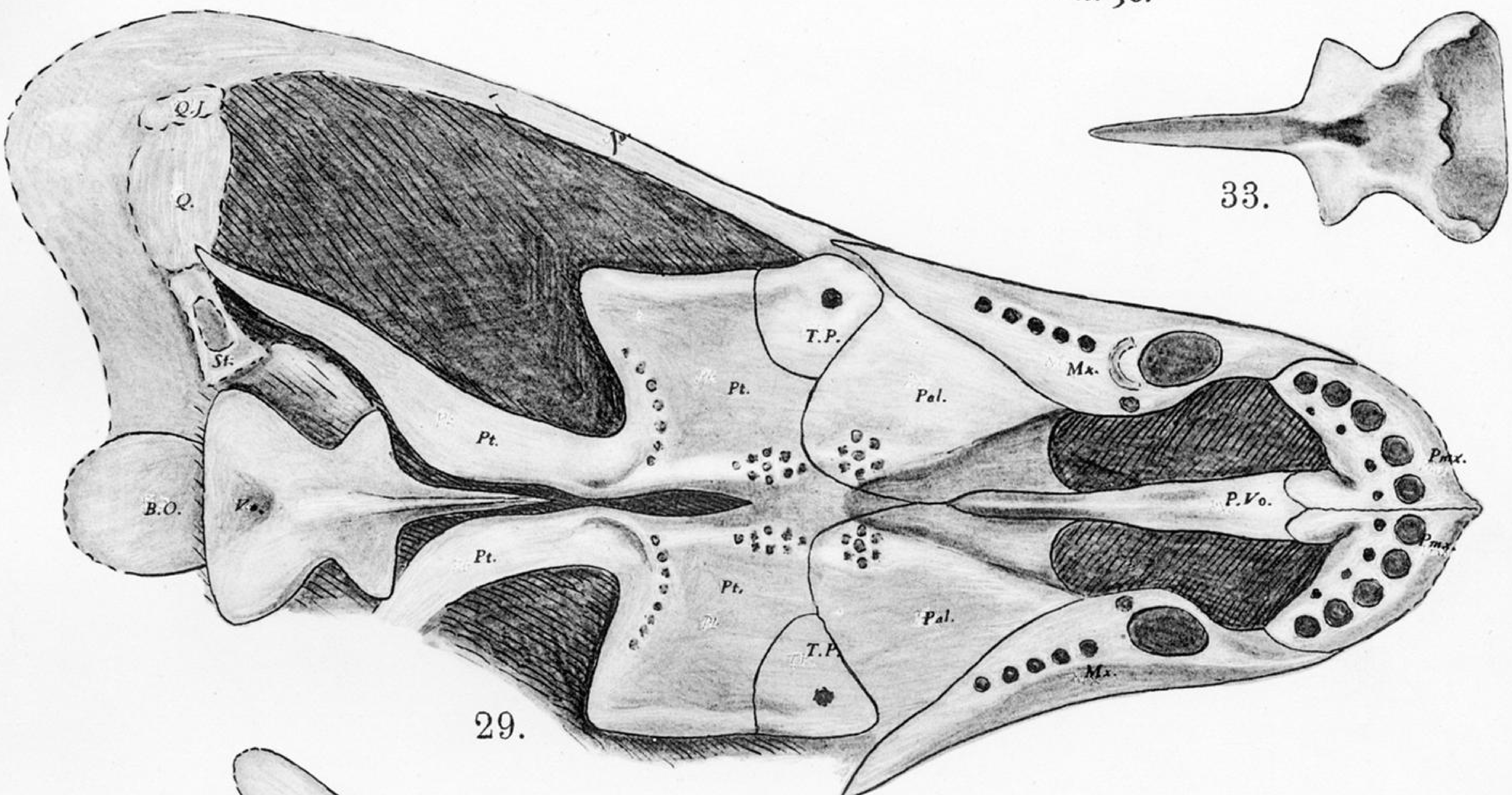


Sect. 36.



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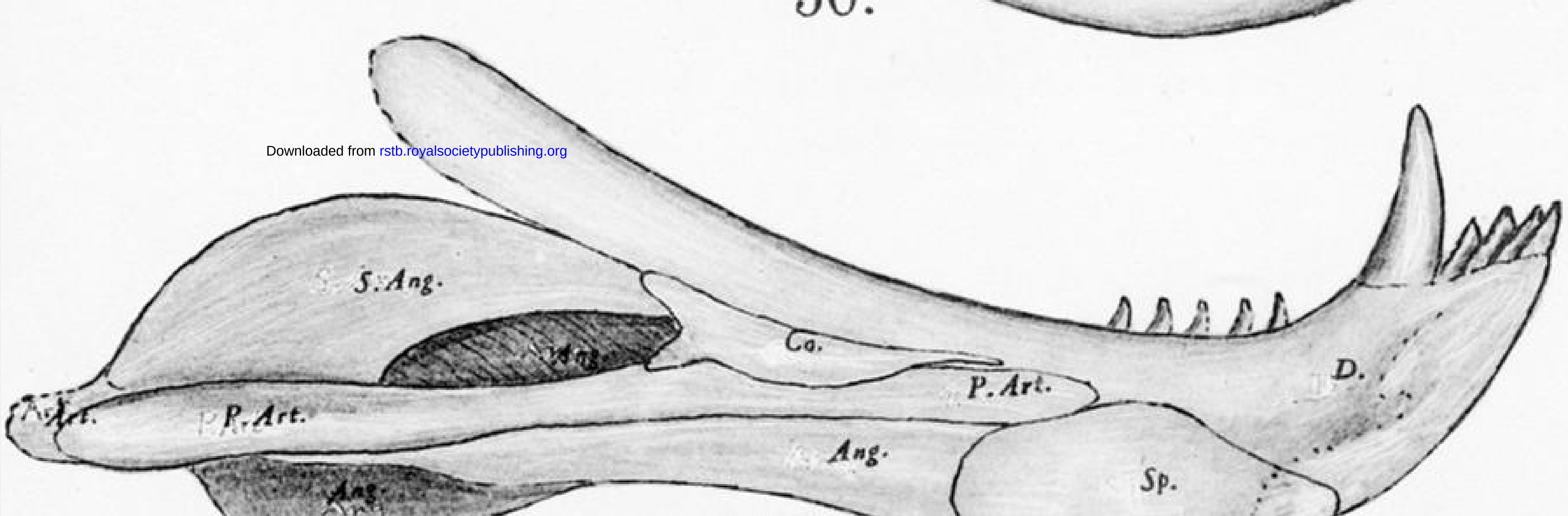

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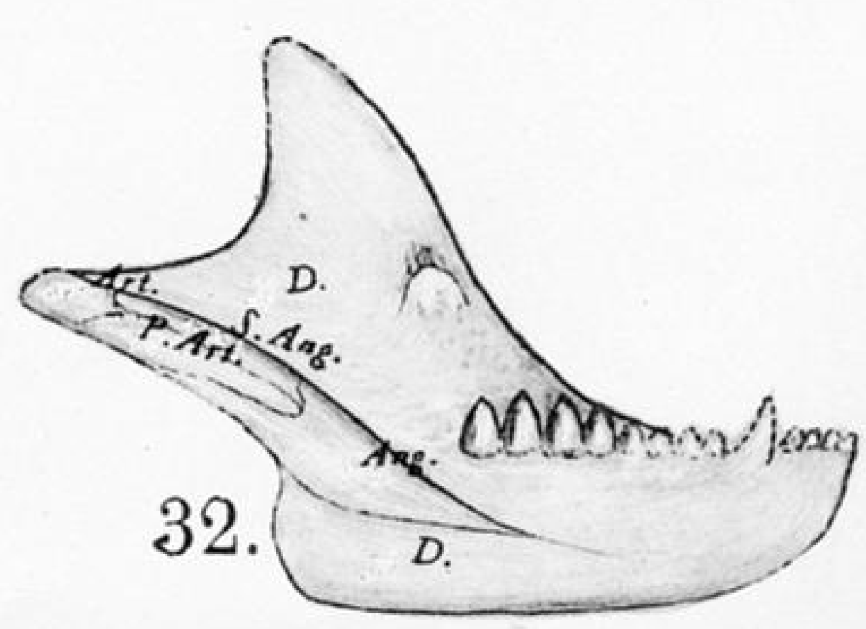


32.

CYNARIOIDES GRACILIS, BROOM.

PLATE 33.

Sections 33–36.—Skull of *Cynarioides gracilis*, BROOM. All twice natural size. Described in the paper.

FIG. 29.—Reconstruction of Palate of *C. gracilis*, BROOM. Twice natural size.

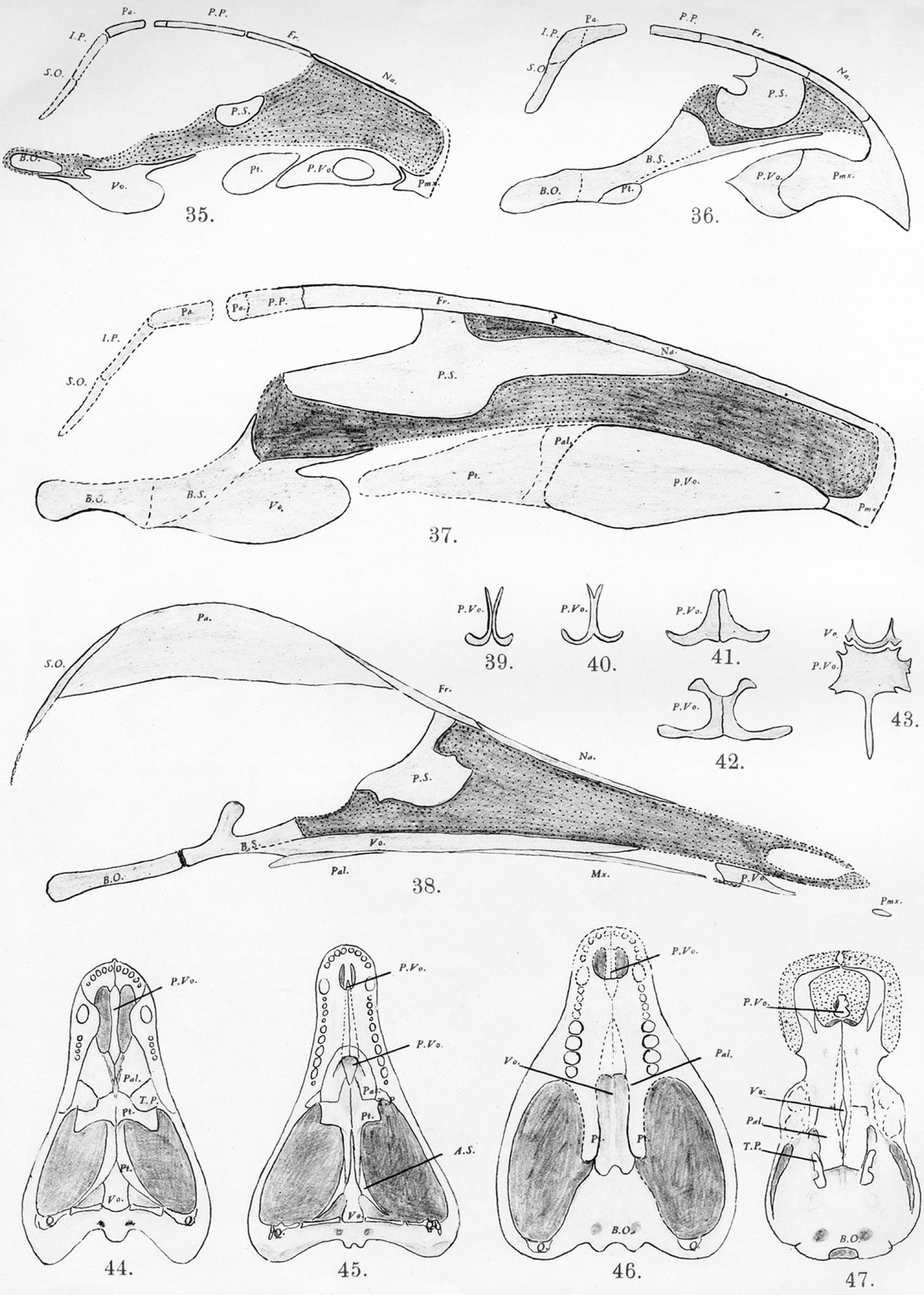
FIG. 30.—Reconstruction of outer side of Mandible of *C. gracilis*, BROOM. One and a-half times natural size.

FIG. 31.—Reconstruction of inner side of Mandible of *C. gracilis*, BROOM. One and a-half times natural size.

FIG. 32.—Inner side of Mandible of a Cave Sandstone Therapsid showing the great reduction of the bones other than the dentary. Natural size.

FIG. 33.—Upper side of vomer of *C. gracilis*, BROOM. Reconstructed from sections. Twice natural size.

FIG. 34.—Side view of vomer of *C. gracilis*, BROOM. Reconstructed from sections. Twice natural size.



RELATIONS OF VOMER AND PREVOMER IN REPTILES AND ORNITHORHYNCHUS.

PLATE 34.

FIG. 35.—Reconstructed median section of the skull of *Cynarioides gracilis*, BROOM. About six-fifths natural size.

FIG. 36.—Median section of skull of young *Dicynodon Sollasi*, BROOM. Natural size.

FIG. 37.—Median section of skull of *Lycænodon longiceps*, BROOM. Natural size. Anterior two-thirds from type specimen. Posterior region restored from crushed specimen which I believe to belong to same species.

FIG. 38.—Median section of skull of young *Ornithorhynchus anatinus*, SHAW. Almost three times natural size.

FIG. 39.—Section across the prevomers of the small Therocephalian *Ictidognathus hemburyi*, BROOM. About three times natural size.

FIG. 40.—Section across the united prevomers of a small undescribed Therocephalian. Enlarged about five times.

FIG. 41.—Section across the prevomers of *Sphenodon punctatus*, GRAY. Enlarged about four times.

FIG. 42.—Section across the prevomers of *Ornithorhynchus anatinus*, SHAW. Enlarged about six times.

FIG. 43.—Section across the united prevomers and the vomer of *Dicynodon platyceps*, BROOM. Natural size.

FIG. 44.—Base of skull (palate) of the Gorgonopsian *Scylacops capensis*, BROOM. Reduced.

FIG. 45.—Base of skull of the Cynodont *Cynidiognathus longiceps*, HAUGHTON. Reduced.

FIG. 46.—Base of skull of undescribed higher Therapsid, Ictidosaurian. Reduced.

FIG. 47.—Base of skull of young *Ornithorhynchus anatinus*, SHAW. Natural size.

(These four views show evolution of prevomers and vomer through the Therapsidæ to the Mammal.)